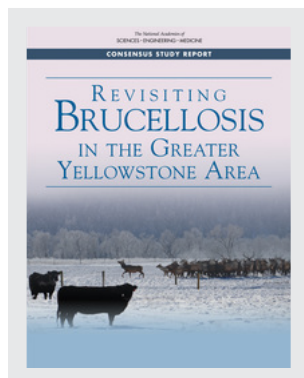


This PDF is available at <http://nap.edu/24750>

SHARE



Revisiting Brucellosis in the Greater Yellowstone Area (2020)

DETAILS

210 pages | 8.5 x 11 | PAPERBACK

ISBN 978-0-309-45831-3 | DOI 10.17226/24750

CONTRIBUTORS

Committee on Revisiting Brucellosis in the Greater Yellowstone Area; Board on Agriculture and Natural Resources; Division on Earth and Life Studies; National Academies of Sciences, Engineering, and Medicine

SUGGESTED CITATION

National Academies of Sciences, Engineering, and Medicine 2020. *Revisiting Brucellosis in the Greater Yellowstone Area*. Washington, DC: The National Academies Press. <https://doi.org/10.17226/24750>.

GET THIS BOOK

FIND RELATED TITLES

Visit the National Academies Press at [NAP.edu](https://nap.edu) and login or register to get:

- Access to free PDF downloads of thousands of scientific reports
- 10% off the price of print titles
- Email or social media notifications of new titles related to your interests
- Special offers and discounts



Distribution, posting, or copying of this PDF is strictly prohibited without written permission of the National Academies Press. (Request Permission) Unless otherwise indicated, all materials in this PDF are copyrighted by the National Academy of Sciences.

Copyright © National Academy of Sciences. All rights reserved.

REVISITING
BRUCELLOSIS
IN THE GREATER
YELLOWSTONE AREA

Committee on Revisiting Brucellosis in the Greater Yellowstone Area

Board on Agriculture and Natural Resources

Division on Earth and Life Studies

A Consensus Study Report of
The National Academies of
SCIENCES • ENGINEERING • MEDICINE

THE NATIONAL ACADEMIES PRESS

Washington, DC

www.nap.edu

THE NATIONAL ACADEMIES PRESS

500 Fifth Street, NW

Washington, DC 20001

This study was supported by Grant #14-9795-2254-GR between the National Academy of Sciences and the U.S. Department of Agriculture's Animal and Plant Health Inspection Service. Any opinions, findings, conclusions, or recommendations expressed in this publication do not necessarily reflect the views of any organization or agency that provided support for the project.

International Standard Book Number-13: 978-0-309-45831-3

International Standard Book Number-10: 0-309-45831-5

Digital Object Identifier: <https://doi.org/10.17226/24750>

Additional copies of this publication are available from the National Academies Press, 500 Fifth Street, NW, Keck 360, Washington, DC 20001; (800) 624-6242 or (202) 334-3313; <http://www.nap.edu>.

Copyright 2020 by the National Academy of Sciences. All rights reserved.

Printed in the United States of America

Cover photo courtesy of Mark Gocke, Wyoming Game & Fish Department.

Suggested citation: National Academies of Sciences, Engineering, and Medicine. 2020. *Revisiting Brucellosis in the Greater Yellowstone Area*. Washington, DC: The National Academies Press. <https://doi.org/10.17226/24750>.

The National Academies of **SCIENCES • ENGINEERING • MEDICINE**

The **National Academy of Sciences** was established in 1863 by an Act of Congress, signed by President Lincoln, as a private, nongovernmental institution to advise the nation on issues related to science and technology. Members are elected by their peers for outstanding contributions to research. Dr. Marcia McNutt is president.

The **National Academy of Engineering** was established in 1964 under the charter of the National Academy of Sciences to bring the practices of engineering to advising the nation. Members are elected by their peers for extraordinary contributions to engineering. Dr. John L. Anderson is president.

The **National Academy of Medicine** (formerly the Institute of Medicine) was established in 1970 under the charter of the National Academy of Sciences to advise the nation on medical and health issues. Members are elected by their peers for distinguished contributions to medicine and health. Dr. Victor J. Dzau is president.

The three Academies work together as the **National Academies of Sciences, Engineering, and Medicine** to provide independent, objective analysis and advice to the nation and conduct other activities to solve complex problems and inform public policy decisions. The National Academies also encourage education and research, recognize outstanding contributions to knowledge, and increase public understanding in matters of science, engineering, and medicine.

Learn more about the National Academies of Sciences, Engineering, and Medicine at www.nationalacademies.org.

The National Academies of
SCIENCES • ENGINEERING • MEDICINE

Consensus Study Reports published by the National Academies of Sciences, Engineering, and Medicine document the evidence-based consensus on the study's statement of task by an authoring committee of experts. Reports typically include findings, conclusions, and recommendations based on information gathered by the committee and the committee's deliberations. Each report has been subjected to a rigorous and independent peer-review process and it represents the position of the National Academies on the statement of task.

Proceedings published by the National Academies of Sciences, Engineering, and Medicine chronicle the presentations and discussions at a workshop, symposium, or other event convened by the National Academies. The statements and opinions contained in proceedings are those of the participants and are not endorsed by other participants, the planning committee, or the National Academies.

For information about other products and activities of the National Academies, please visit www.nationalacademies.org/about/whatwedo.

COMMITTEE ON REVISITING BRUCELLOSIS IN THE GREATER YELLOWSTONE AREA¹

Chair

TERRY F. McELWAIN (NAM²), Washington State University

Members

L. GARRY ADAMS, Texas A&M University

CYNTHIA L. BALDWIN, University of Massachusetts Amherst

MICHAEL B. COUGHENOUR, Colorado State University

PAUL C. CROSS, U.S. Geological Survey

RICHARD D. HORAN, Michigan State University

DAVID A. JESSUP, University of California, Davis

DUSTIN P. OEDEKOVEN, South Dakota Animal Industry Board

DAVID W. PASCUAL, University of Florida

VALERIE E. RAGAN, Virginia-Maryland College of Veterinary Medicine

GLYNN T. TONSOR, Kansas State University

Staff

PEGGY TSAI YIH, Study Director and Senior Program Officer

JENNA BRISCOE, Research Assistant

ROBIN A. SCHOEN, Director, Board on Agriculture and Natural Resources

¹ Staff and affiliations current as of 2015.

² National Academy of Medicine.

BOARD ON AGRICULTURE AND NATURAL RESOURCES¹

Chair

CHARLES W. RICE, Kansas State University, Manhattan

Members

SUSAN CAPALBO, Oregon State University, Corvallis
GAIL CZARNECKI-MAULDEN, Nestlé Purina PetCare, St. Louis, MO
GEBISA EJETA, Purdue University, West Lafayette, IN
ROBERT B. GOLDBERG (NAS²), University of California, Los Angeles
FRED GOULD (NAS²), North Carolina State University, Raleigh
MOLLY M. JAHN, University of Wisconsin–Madison
ROBBIN S. JOHNSON, Cargill Foundation, Wayzata, MN
JAMES W. JONES (NAE³), University of Florida, Gainesville
A.G. KAWAMURA, Solutions from the Land, Washington, DC
STEPHEN S. KELLEY, North Carolina State University, Raleigh
JULIA L. KORNEGAY, North Carolina State University, Raleigh
JIM E. RIVIERE (NAM⁴), Kansas State University, Manhattan

Staff

ROBIN A. SCHOEN, Director
CAMILLA YANDOC ABLES, Senior Program Officer
JENNA BRISCOE, Research Assistant
KARA N. LANEY, Senior Program Officer
PEGGY TSAI YIH, Senior Program Officer

¹ Staff and affiliations current as of 2015.

² National Academy of Sciences.

³ National Academy of Engineering.

⁴ National Academy of Medicine.

Reviewers

This Consensus Study Report was reviewed in draft form by individuals chosen for their diverse perspectives and technical expertise. The purpose of this independent review is to provide candid and critical comments that will assist the National Academies of Sciences, Engineering, and Medicine in making each published report as sound as possible and to ensure that it meets the institutional standards for quality, objectivity, evidence, and responsiveness to the study charge. The review comments and draft manuscript remain confidential to protect the integrity of the deliberative process.

We thank the following individuals for their review of this report:

Mark S. Boyce, University of Alberta
Norman Cheville, Iowa State University
Andrew Dobson, Princeton University
Francis D. Galey, University of Wyoming
Robert Garrett, Montana State University
Colin Gillin, Oregon Department of Fish and Wildlife
N. Thompson Hobbs, Colorado State University
Bret Marsh, Indiana State Board of Animal Health
Michael W. Miller, Colorado Parks & Wildlife
Robert Nordgren, Merial
Daniel O'Brien, Michigan Department of Natural Resources
Gary Splitter, University of Wisconsin
Michael Springborn, University of California, Davis

Although the reviewers listed above provided many constructive comments and suggestions, they were not asked to endorse the conclusions or recommendations of this report nor did they see the final draft before its release. The review of this report was overseen by **Gordon H. Orians**, University of Washington, and **James E. Womack**, Texas A&M University. They are responsible for making certain that an independent examination of this report was carried out in accordance with the standards of the National Academies and that all review comments were carefully considered. Responsibility for the final content rests entirely with the authoring committee and the National Academies.

Preface

With a global incidence of more than half a million human cases annually, brucellosis is a zoonotic disease of public health concern for much of the world. Fortunately, due in large part to the brucellosis eradication program begun by the U.S. Department of Agriculture (USDA) more than 80 years ago, the incidence of human brucellosis in the United States is now less than 0.5 cases/million population, a dramatic reduction from the high of more than 6,000 cases annually in 1947. Unlike in 1947, nearly all U.S. human brucellosis cases are now caused by *Brucella melitensis*, acquired while traveling outside the United States, not *B. abortus*.

The only remaining U.S. reservoir of *B. abortus* infection is in the Greater Yellowstone Area (GYA), where wildlife-transmitted cases spill over into domestic cattle and domestic bison. Yet this spillover is now occurring with increasing frequency, raising the possibility of brucellosis reoccurrence outside the GYA. This report examines the changing dynamic of brucellosis in the GYA, providing a comprehensive update of what is new since the 1998 National Research Council report *Brucellosis in the Greater Yellowstone Area* and exploring various options for addressing the challenge of brucellosis disease management.

Much has changed in the 20 years since the previous report. There is now clear evidence that transmission of *B. abortus* to domestic livestock in the GYA has come from infected elk, not bison, posing greater challenges for control of transmission to domestic species. This is coupled with significant changes in land use around the GYA, and the increasing value that the public places on our wildlands and the wildlife they support. Indeed, change has been the norm, even during the course of the committee's deliberations. New cases have been recognized in cattle and domestic bison since the start of the study. Policies of state agencies trying to counter the increasing incidence of brucellosis have changed. The study was conducted during the 100th anniversary year of the national park system, with Yellowstone National Park (YNP) the "granddaddy" of them all. And the bison, an icon of YNP and a key player in brucellosis control, was officially designated as our national mammal, further raising the visibility of brucellosis management efforts in the GYA.

The committee gained insight from invited speakers and an impassioned audience expressing multiple perspectives in public meetings. In addition to the study's sponsor, USDA, stakeholders range from additional federal and state agencies to nongovernmental organizations, and from the public who gain value and satisfaction from our wildlands and the animals they support to those who have for generations derived their livelihoods from privately owned land in and around the GYA. All are impacted by efforts to manage brucellosis caused by *B. abortus* in the last remaining disease reservoir. There is a complexity and an interdependency in addressing the issue that mirrors the complexity of the ecosystem in which brucellosis occurs and which defies both simple solutions and a perfect solution. The committee has taken an objective, science-based approach in addressing its Statement of Task and presents this report as a comprehensive starting point for discussions among all stakeholders to address a problem of increasing concern. We trust this report will be helpful in those deliberations.

I would like to express thanks to all the committee members for their dedication and perseverance during the long course of the committee's deliberations and writing. On behalf of the committee, sincere thanks are also extended to the study director, Peggy Tsai Yih, who did an outstanding job of directing a challenging task, and to Robin A. Schoen and Jenna Briscoe, who provided background support for the study. As always, a National Academies report does not simply happen de novo and capable hands guide

Preface

the process throughout. Lastly, the committee thanks all those who provided input during multiple public meetings and to those who provided answers in response to what may at times have seemed like an endless list of questions and requests. We are grateful for your efforts in supporting this report.

Terry F. McElwain, *Chair*
Committee on Revisiting Brucellosis
in the Greater Yellowstone Area

Contents

SUMMARY	1
1 INTRODUCTION	10
Background, 10	
The Greater Yellowstone Area, 11	
Administrative Complexity of the Greater Yellowstone Area, 14	
Purpose of This Study, 15	
Approach to the Task, 15	
Organization of the Report, 16	
References, 17	
2 GEOGRAPHIC SCOPE OF POPULATIONS AND DISEASE AND CHANGE IN LAND USE	19
Introduction, 19	
Elk Populations and Distributions, 19	
Changes in Land Use and Consequences for Elk, 32	
Bison Populations and Distributions, 33	
Livestock, 38	
Implications of Changing Climate for Elk and Bison, 39	
Summary, 41	
References, 42	
3 ECOLOGY AND EPIDEMIOLOGY OF <i>BRUCELLA ABORTUS</i> IN THE GREATER YELLOWSTONE ECOSYSTEM	48
Review of Brucellosis Cases Since 1998, 48	
Disease Dynamics in Bison and Elk, 51	
Effects of Population Size and Aggregation on Bison and Elk Transmission, 56	
Supplemental Feedgrounds, 59	
Potential Effects of Predators and Scavengers on Brucellosis, 60	
Effect of Disease on Bison and Elk Populations, 61	
References, 62	
4 SCIENTIFIC PROGRESS AND NEW RESEARCH TOOLS	65
Infection Biology and Pathogenesis of <i>B. abortus</i> in Cattle, Bison, and Elk, 65	
Diagnostics, 67	
Commercial Vaccines in Wildlife, 71	
New Scientific Tools Informing Brucellosis Infection Biology, Pathogenesis, and Vaccinology, 74	
Conclusion, 75	
References, 75	

Contents

5	FEDERAL, STATE, AND REGIONAL MANAGEMENT EFFORTS	83
	Brief Historical Overview of Brucellosis Control Efforts, 83	
	Changes in Status and Classification of States, 83	
	Regional and National Control Programs, 84	
	Interagency Cooperative Bodies, 90	
	Surveillance, 92	
	Bison Separation and Quarantine, 95	
	Costs of Programs, 95	
	References, 98	
6	ADAPTIVE MANAGEMENT	101
	Defining Adaptive Management, 101	
	Adaptive Management in the Greater Yellowstone Area: Case Studies, 103	
	References, 106	
7	MANAGEMENT OPTIONS.....	110
	Introduction, 110	
	Incentivizing Risk Mitigation Efforts, 110	
	Use of Feedgrounds, 111	
	Hunting of Wildlife, 113	
	Land Use, 116	
	Zoning Using Designated Surveillance Areas, 117	
	Test and Remove, 118	
	Vaccines and Delivery Systems for Cattle, Bison, and Elk, 120	
	Sterilization and Contraceptives, 121	
	Predation and Scavengers, 122	
	References, 123	
8	ECONOMIC ISSUES IN MANAGING BRUCELLOSIS.....	128
	Introduction, 128	
	Bioeconomic Framework, 129	
	Economic Efficiency in a Dynamic, Coupled System, 137	
	Promoting Private Disease Control Efforts, 143	
	Summary, 148	
	References, 148	
9	REMAINING GAPS FOR UNDERSTANDING AND CONTROLLING BRUCELLOSIS	153
	Introduction, 153	
	Disease Ecology, 153	
	Economics, 154	
	Immunology, 155	
	Vaccines and Delivery Mechanisms, 157	
	Genotyping and Genetics, 159	
	Diagnostics, 161	
	References, 163	
10	OVERALL FINDINGS, CONCLUSIONS, AND RECOMMENDATIONS	169
	What's New Since 1998?, 169	
	Adopting an Active Adaptive Management Approach, 170	
	Adaptive Management Options to Reduce Risk, 171	

Contents

Bioeconomics: A Framework for Making Decisions, 179	
A Call to Strategic Action, 179	
Research Agenda, 182	
Concluding Remarks, 185	
References, 185	

APPENDIXES

A	BIOGRAPHICAL SKETCHES OF COMMITTEE MEMBERS	187
B	OPEN SESSION MEETING AGENDAS.....	191

BOXES, FIGURES, AND TABLES

BOXES

1-1	Statement of Task, 16
7-1	Land Management Risk Assessment to Reduce Disease Risks, 112

FIGURES

1-1	Map of the GYA by jurisdiction, 12
1-2	Map showing the GYA boundary and designated surveillance areas as of 2016, 13
2-1	Map of migration corridors, winter ranges and summer ranges of 9 of 11 major elk herds in the GYA, 20
2-2	Northern Yellowstone elk numbers, 21
2-3	Elk numbers and percentages north of YNP and on Dome Mountain, 22
2-4	Elk management units in Montana, elk hunt units in Wyoming, and game management units in Idaho in relation to the designated surveillance area and the YNP boundary, as of 2014, 25
2-5	Trends in elk numbers in Montana EMUs, 26
2-6	Histogram of the elk group size distribution from the eastern portion of the GYA in Wyoming, 27
2-7	Elk population trends in herds east of YNP, 28
2-8	Elk population trends in herds south and southeast of YNP, 29
2-9	Elk population trends in herds the furthest south of YNP, 29
2-10	Bison range distribution conservation areas and Zone 2 bison tolerance areas, 34
2-11	Bison counts and annual removals, northern and central herds, 35
2-12	Bison population growth rates versus population sizes in the previous year, northern and central herds, 37
2-13	Grazing allotments throughout the GYA, 39
2-14	Active U.S. Forest Service grazing allotments in Bridger-Teton National Forest, 40
3-1	Number of cattle and domestic bison herds infected with <i>B. abortus</i> in the GYA by state from 1990 to 2016, 48
3-2	States to which animals leaving Brucellosis-affected herds in the GYA were traced, 2002-2016, 52
3-3	Maps of seroprevalence in elk using data prior to 2000 and from 2010 to 2015, 53
3-4	Maps of sampling effort in elk prior to 2000 and from 2010 to 2015, 53
3-5	Elk seroprevalence in the East Madison Hunt District (HD) 362 and Gardiner Area HD 313, 54
3-6	Elk seroprevalence in the Cody and Clarks Fork regions of Wyoming, 55

Contents

3-7	Elk seroprevalence in the South Wind River and West Green River regions of Wyoming, both of which are south and adjacent to regions with supplemental feedgrounds, 55
3-8	Elk seroprevalence over time for two management units in Idaho, District 66A, District 76, 56
3-9	Elk seroprevalence over time for management units in Idaho where the seroprevalence may be increasing (Districts 61, 62, and 67), 57
3-10	Elk seroprevalence over time for several management units in Idaho (Districts 64, 65, and 66) that are too weakly sampled to assess any temporal trends, 58
4-1	The Greater Yellowstone Area tristate schematic for serological testing of elk, 70
5-1	Seroprevalence of <i>B. abortus</i> in elk by year for test and slaughter pilot project at Muddy Creek Feedground, 89
5-2	Efficacy of elk <i>Brucella</i> strain 19 vaccination, 90
8-1	A bioeconomic assessment of economic costs and benefits, 130

TABLES

2-1	Elk Numbers in EMUs (Hunting Districts) North and Northwest of YNP, But Within the Brucellosis DSA, in 2015, 24
2-2	Numbers of Elk in Herds East of YNP in Wyoming in 2015, 27
2-3	Numbers of Elk in Herds South and Southeast of YNP in Wyoming in 2015, 28
2-4	Elk Herds in Idaho in the GYA, 30
3-1	Brucellosis Herds Detected in the GYA, 2002-2016, 49
4-1	Summary of RB51's Efficacy in Bison, 73
5-1	Federal Agency Jurisdiction and Involvement in Brucellosis, 85
5-2	State Agency Jurisdiction and Involvement in Brucellosis, 88
5-3	Estimated Number of Samples Collected by Slaughter Plant for FY2017 (October 1, 2016, through September 30, 2017), 94

Summary

BACKGROUND

Brucellosis is a nationally and internationally regulated disease of livestock with significant consequences for animal health, public health, and international trade. In cattle, the primary cause of brucellosis is *Brucella abortus*, a zoonotic bacterial pathogen that also affects wildlife, including bison and elk. While *B. abortus* can cause both acute febrile and chronic relapsing brucellosis in humans, it is no longer a major human health concern in the United States due largely to public health interventions such as the pasteurization of milk and the successful efforts of the Brucellosis Eradication Program that began in 1934.

As a result of the decades long eradication program, most of the country is now free of bovine brucellosis. The Greater Yellowstone Area (GYA), where brucellosis is endemic in bison and elk, is the last known *B. abortus* reservoir in the United States. The GYA is home to more than 5,500 bison that are the genetic descendants of the original free-ranging bison herds that survived in the early 1900s, and home to more than 125,000 elk whose habitats are managed through interagency efforts, including the National Elk Refuge (NER) and 22 supplemental winter feedgrounds maintained in Wyoming.

Since the National Research Council (NRC) issued the 1998 report *Brucellosis in the Greater Yellowstone Area*, brucellosis has re-emerged in domestic cattle and bison herds in the GYA; from 1998-2016, 22 cattle herds and 5 privately owned bison herds were affected in Idaho, Montana, and Wyoming. During the same time period, all other states in the United States achieved and maintained brucellosis class-free status. A 2010 interim rule to regionalize brucellosis control enabled the three GYA states to create designated surveillance areas (DSAs) to monitor brucellosis in specific zones and to reduce the economic impact for producers in non-affected areas. However, brucellosis has expanded beyond the original DSAs, resulting in the outward adjustment of DSA boundaries. Although most cattle in the GYA are vaccinated with *B. abortus* strain RB51, it does not necessarily prevent infection but it does reduce abortions. The increase in cattle infections in the GYA, coupled with the spread in wildlife, has been alarming for producers in the area; moreover, the risk of additional spread from movement of GYA livestock to other areas across the United States is increasing due to the lack of guidance and surveillance, with the potential for spread and significant economic impact outside the GYA.

SCOPE AND APPROACH TO THE REVIEW

The 1998 NRC report reviewed the scientific knowledge regarding *B. abortus* transmission among wildlife—particularly bison and elk—and cattle in the GYA. Given the scientific and technological advances in the two decades since that first report, the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) requested that the National Academies of Sciences, Engineering, and Medicine (the National Academies) revisit the issue of brucellosis in the GYA. The primary motivation for USDA-APHIS in requesting the study was to understand the factors associated with the increased transmission of brucellosis from wildlife to livestock, the recent apparent expansion of brucellosis in non-feedground elk, and the desire to have science inform the course of any future actions in addressing brucellosis in the GYA. Although USDA-APHIS commissioned the study to inform its brucellosis eradication strategy, there are additional federal and state agencies that each have authority across state, federal, private, and tribal lands that course through the GYA. Also, Yellowstone National Park (YNP) is a national icon. American bison were recently designated as the national mammal, and the subject of brucellosis is of interest to many groups with economic interests in wildlife and livestock in the GYA.

*Revisiting Brucellosis in the Greater Yellowstone Area***CONCLUSIONS AND RECOMMENDATIONS****A New Focus on Elk**

In tracing the genetic lineage of *Brucella* across the ecosystem and among species, elk are now recognized as a primary host for brucellosis and have been the major transmitter of *B. abortus* to cattle. All recent cases of brucellosis in GYA cattle are traceable genetically and epidemiologically to transmission from elk, not bison. The seroprevalence of brucellosis in elk in some regions has been increasing from what were historically low levels, and data strongly suggest that elk are able to maintain brucellosis infection within their populations that have limited to no direct contact with the feedgrounds or with infected bison. Direct contact of elk with cattle is more prevalent than contact of cattle with bison. As a result, the risk of transmission from elk to cattle may be increasing.

In contrast, there have been no cases of transmission from GYA bison to cattle in the 27 herds infected with brucellosis since 1998 despite no change in the seroprevalence of brucellosis in bison. This is likely a result of bison management practices outlined in the Interagency Bison Management Plan (IBMP) combined with fewer cattle operations in the GYA region where bison leave YNP.

Ecological changes within the GYA since 1998 have shifted the dynamics of wildlife populations. The reintroduction of wolves and increases in grizzly bear numbers have impacted the density and distribution of elk. Elk populations have expanded on the periphery of the GYA but have decreased inside YNP. The rising number of private landowners has changed how land is used around national parks, with private lands increasingly serving as refugia for elk from hunting.

With elk now viewed as the primary source for new cases of brucellosis in cattle and domestic bison, the committee concludes that brucellosis control efforts in the GYA will need to sharply focus on approaches that reduce transmission from elk to cattle and domestic bison (Conclusion 1).

Recommendation 1: To address brucellosis in the GYA, federal and state agencies should prioritize efforts on preventing *B. abortus* transmission by elk. Modeling should be used to characterize and quantify the risk of disease transmission and spread from and among elk, which requires an understanding of the spatial and temporal processes involved in the epidemiology of the disease and economic impacts across the GYA. Models should include modern, statistically rigorous estimates of uncertainty.

Adopting an Active Adaptive Management Approach

Many brucellosis management efforts implemented since the 1998 report may appear to have taken an adaptive management approach; however, those efforts have not followed the basic tenet of employing an *active* approach. More specifically, individual management actions were not designed or established to allow for scientific assessment of effectiveness, which is a central tenet of active adaptive management. Management activities are typically conducted as hypothesis testing, the outcome of which directs subsequent decisions and actions toward the ultimate goal. In the absence of carefully designed management actions that include experimental controls, it is difficult to determine the effectiveness of a particular practice, leading to a slower learning process.

Recommendation 2: In making timely and data-based decisions for reducing the risk of *B. abortus* transmission from elk, federal and state agencies should use an *active* adaptive management approach that would include iterative hypothesis testing and mandated periodic scientific assessments. Management actions should include multiple, complementary strategies over a long period of time and should set goals demonstrating incremental progress toward reducing the risk of transmission from and among elk.

Summary

Adaptive Management Options to Reduce Risk

No single management approach can independently result in reducing risk to a level that will prevent transmission of *B. abortus* among wildlife and domestic species (Conclusion 2). To consider any approach in isolation is to miss the bigger picture of a highly interconnected ecosystem and a broader understanding of various factors affecting risk that have evolved since 1998. While there are knowledge gaps that limit understanding of actual risk, the options below are possible adaptive management approaches to reduce risk of *B. abortus* transmission and to inform future risk management plans. These approaches would need to be based on an integrated assessment of risk and costs, but they do not necessarily need to be applied uniformly over space and time.

Population Reduction

Reducing the population size of cattle, bison, or elk are all likely to reduce the risk of brucellosis transmission to cattle by reducing the area of potential contact or the number of infected individuals in those areas, even if the disease prevalence in the wildlife hosts remains constant. However, each species has a constituency that would likely oppose any population reduction.

Elk: Reducing the elk population is an option for reducing the risk of transmission among elk, cattle, and bison. Unlike bison, transmission among elk appears to be influenced by density. **Thus, reducing elk group sizes and/or density may decrease elk seroprevalence over time among and potentially decrease the risk of elk transmission (Conclusion 3).** Potential management approaches for elk population reduction include the following:

- *Hunting.* Hunting is currently used to control elk populations, with management unit population targets set as a balance of public demand and population goals. Hunting could also be used as a means of incentivizing targeted population reductions based on brucellosis risk. Additional and ongoing assessments of the efficacy of these approaches would be needed as part of an active adaptive management approach.
- *Contraception.* GonaCon™ is an immunocontraceptive that targets high-risk females; contraception would need to be viewed as experimental in elk but, as in bison, there is potential in significantly reducing the elk population and prevalence of brucellosis in elk.
- *Test and removal.* Test and removal has been an invaluable part of the brucellosis eradication program for domestic species. As with domestic species, test and removal in elk would need to be part of an integrated program combined with other tools such as quarantine, herd management to reduce intra-herd transmission, and vaccination.

Bison: While the primary focus would be on elk, bison remain an important reservoir for brucellosis. If further reducing the prevalence of brucellosis in bison is desirable, these bison population control measures could potentially be considered:

- *Removal of infected bison.* Population reduction alone is not likely to reduce brucellosis prevalence in bison since transmission is frequency dependent rather than density dependent. **For this reason, if reduction of brucellosis prevalence is a goal, removal of bison for population management purposes will need to target brucellosis-infected individuals whenever possible (Conclusion 4).**
- *Quarantine and relocation.* Sufficient evidence is now available to also include separation and quarantine of test negative bison as a management action, allowing for the eventual relocation of GYA bison to other bison herds (including onto tribal lands).

Revisiting Brucellosis in the Greater Yellowstone Area

- *Targeted removal within YNP.* While this option may not be politically, logistically, socially, or economically feasible, targeted removal of seropositive bison (which would be facilitated by the use of a pen-side assay) or high-risk bison (such as young, pregnant females) within YNP in the winter could reduce the need for large culls of bison populations that move outside YNP. This could also reduce the episodic swings in the bison population and winter emigrations from YNP that lead to large culls in some years.
- *Bison genetics.* Test and removal of bison provides a valuable opportunity to preserve genetic material and live cells for future use in establishing brucellosis negative and potentially disease resistant bison through cloning techniques.
- *Contraception.* Experimental and modeling results in bison suggest that contraception using a gonadotropin releasing hormone immunocontraceptive (i.e., GonaCon™) may help in reducing the prevalence of brucellosis. This approach targets high-risk females, preventing pregnancy and thus abortion and birthing events that increase risk of transmission through shedding of high numbers of bacteria.

Intervention Options Within Feedgrounds

The role of the NER and Wyoming elk supplemental winter feedgrounds in maintaining and propagating brucellosis in the GYA is a controversial topic. Feedgrounds have been useful for conservation and hunting purposes and for separating elk from cattle. However, it is widely accepted that feedgrounds promote transmission of *B. abortus* among elk and are likely responsible for causing and maintaining elevated seroprevalence in those areas.

The potential options below for management interventions in feedgrounds could be further evaluated using an active adaptive management approach, with the interventions applied singularly or in combination.

- *Balance the timing and use of feedgrounds.* Data suggest that ceasing feeding earlier in the season on feedgrounds to encourage dispersal would result in less risk of infection among elk (and bison where intermixing occurs), because calving of elk would occur in a more natural environment away from the dense population present in feedgrounds.
- *Feeding patterns on feedgrounds.* Data suggest that feeding in checkerboard patterns and spreading feed more broadly appear to reduce elk-to-elk contact, and therefore potentially reduce transmission risk.
- *Test and removal on feedgrounds.* The Muddy Creek feedground pilot project provided an example of temporarily reducing seroprevalence of brucellosis through test and removal of infected female elk. Its use would be limited to very specialized conditions (e.g., in reducing feedground density) as large populations appear to be able to maintain a brucellosis reservoir outside the feedgrounds.
- *Contraception in elk.* The feedgrounds provide an opportunity to more easily access female elk for contraceptive application.
- *Removal of aborted fetuses.* Abortion on feedgrounds offers an opportunity to remove aborted fetuses on a daily basis and to disinfect the abortion site using an appropriate disinfectant, thus reducing the likelihood of transmission to other elk.
- *Other future interventions.* Given the enormity of the challenge in accessing elk in the vastness of the open West, feedgrounds offer a unique opportunity to intervene in a relatively smaller land area where elk are concentrated and capture is easier, less dangerous for personnel, and less costly.

Summary

Incremental Closure of Feedgrounds

Closure of feedgrounds appears to be an obvious approach to control brucellosis in the GYA, but there are impacts of feedground closure that will need to be considered and assessed. First, while there is still some uncertainty, scientific evidence suggests that brucellosis in elk is self-sustaining in some areas without continuous reintroduction of infected feedground elk. If future work continues to support this conclusion, it is possible that closure of feedgrounds would not have any impact on brucellosis prevalence in more remote elk populations away from the feedgrounds. Closure of feedgrounds would, however, potentially reduce the “seeding” of new areas with infected elk where a reservoir does not currently exist. Second, anecdotal evidence suggests that feedgrounds reduce exposure of cattle to infected elk during the high-risk period of abortion or calving. Observational data to support this notion are weak at present. Thus, an unintended outcome of closing feedgrounds could be increased exposure of cattle to infected elk if cattle are turned onto grazing areas at the time that elk are calving. **The weight of evidence nonetheless suggests that reduced use or incremental closure of feedgrounds could benefit elk health in the long term and could reduce the overall prevalence of brucellosis in elk on a broad population basis (Conclusion 5).**

The closure of feedgrounds is likely to bring increased short-term risk due to the potential for increased elk-cattle contact while the seroprevalence in elk remains high. In the longer term, closing feedgrounds may result in reduced elk seroprevalence. **Reduced use or incremental closure of feedgrounds is not a stand-alone solution to control of brucellosis in the GYA and will need to be coupled with other management actions to address the problem at a systems level (Conclusion 6).**

Recommendation 3: Use of supplemental feedgrounds should be gradually reduced. A strategic, stepwise, and science-based approach should be undertaken by state and federal land managers to ensure that robust experimental and control data are generated to analyze and evaluate the impacts of feedground reductions and incremental closure on elk health and populations, risk of transmission to cattle, and brucellosis prevalence.

Spatial and Temporal Separation

One of the fundamental principles of infectious disease control is spatial and temporal separation of individuals and groups to reduce the risk of transmission. Bison management to prevent brucellosis transmission has been successful in part due to spatial and temporal separation from cattle, both because bison are largely contained within YNP and Grand Teton National Park, and when outside the parks they are managed to reduce cattle contact.

Recommendation 4: Agencies involved in implementing the IBMP should continue to maintain a separation of bison from cattle when bison are outside YNP boundaries.

Spatial and temporal separation also plays an important role in reducing transmission risk from elk. Separation of susceptible and infected animals during high-risk periods has been and should continue to be utilized as a risk reduction tool; it is further discussed in the report in the context of specific management approaches. National policy for responding to the identification of infected cattle and domestic bison herds includes time-tested approaches toward maintaining separation of infected and susceptible animals, including hold orders and quarantine during follow-up testing. These actions are valuable tools for reducing risk. Other options include the timing and use of grazing allotments, biosecurity measures, and hazing of elk. Removal of bison for population management purposes could target *B. abortus*-infected individuals if further reducing the prevalence of brucellosis is a goal; however, until tools become available that would simultaneously allow for an eradication program in elk, additional aggressive control measures in bison seem unwarranted.

*Revisiting Brucellosis in the Greater Yellowstone Area**Testing, Surveillance, and Designated Surveillance Areas*

Regionalization is now a well-accepted approach to allow subnational disease containment without jeopardizing the disease status of an entire nation. The success of regionalization relies on robust risk assessment, knowledge of the location and extent of infected animals within and immediately outside the boundary of a control zone, and effective boundary management and enforcement.

The DSA zoning concept is a valuable approach toward brucellosis control in the GYA. The successful use of DSAs is dependent on responsible and timely adjustments of DSA boundaries based on adequate surveillance, particularly of elk. There is no federal guidance for conducting wildlife surveillance outside of the DSA at a level required to monitor the geographic expansion of brucellosis in elk. Each state independently conducts wildlife surveillance outside of the DSA, with no uniform data-based guidelines or requirements for states to reference in determining when to expand their DSA as a result of finding infected or exposed wildlife outside of established DSA boundaries. This lack of uniformity in rules and standards has resulted in an uneven approach to surveillance and to establishing boundaries that accurately reflect risk. If DSA boundaries are not expanded in a timely manner in response to finding seropositive wildlife, there is an increased probability that exposed or infected cattle and domestic bison herds in that area may not be detected in time to prevent further spread of infection as cattle and domestic bison are marketed and moved. There is no major slaughter capacity in Montana or Wyoming where surveillance samples can be collected to detect whether brucellosis has expanded in cattle beyond the DSA boundaries. This gap in slaughter surveillance for non-DSA cattle in the GYA states further raises the risk of brucellosis spreading beyond the DSAs.

The lack of data-based guidance and uniformity in conducting wildlife surveillance outside the DSA, the absence of a GYA-focused approach for national surveillance, and the infrequent oversight of state brucellosis management plans in the midst of expanding seroprevalence of elk has increased the risk for spread of brucellosis in cattle and domestic bison outside the DSA boundaries and beyond the GYA (Conclusion 7).

Recommendation 5: In response to an increased risk of brucellosis transmission and spread beyond the GYA, USDA-APHIS should take the following measures:

5A: Work with appropriate wildlife agencies to establish an elk wildlife surveillance program that uses a modeling framework to optimize sampling effort and incorporates multiple sources of uncertainty in observation and biological processes.

5B: Establish uniform, risk-based standards for expanding the DSA boundaries in response to finding seropositive wildlife. The use of multiple concentric DSA zones with, for example, different surveillance, herd management, biosecurity, testing, and/or movement requirements should be considered based on differing levels of risk, similar to current disease outbreak response approaches.

5C: Revise the national brucellosis surveillance plan to include and focus on slaughter and market surveillance streams for cattle in and around the GYA.

Vaccination

Vaccination is a time-tested, proven method of infectious disease control. Brucellosis vaccination has been an important part of the program to eradicate brucellosis from domestic cattle, and it is effective when used in conjunction with other disease management approaches such as quarantine, herd management to reduce intra-herd transmission, and test and removal. **The significant reduction in risk of transmission among vaccinated cattle provides sufficient reason to continue calfhood and adult vaccination of high-risk cattle when coupled with other risk reduction approaches (Conclusion 8).**

An improved vaccine for each of the three species (elk, bison, and cattle) would help suppress and eventually eliminate brucellosis in the GYA. For free-ranging bison and elk, appropriate and cost-effective vaccine delivery systems would be critical. However, until the issue of infected elk transmitting *B. abortus*

Summary

to cattle is fully addressed, there will still be a perception of risk by other states that would likely drive continued testing of cattle leaving DSAs even if cattle are vaccinated with a highly effective vaccine.

Bioeconomics: A Framework for Making Decisions

Economic resources for managing disease risks in the GYA are scarce. Any management strategies that impose costs on agencies and other stakeholders while producing few benefits will not be adopted. Costs are not limited to direct monetary costs of undertaking management actions, and benefits are not limited to reduced economic risks to cattle producers; the costs and benefits also include the positive and negative impacts to the ecological processes of the region that are directly or indirectly valued by stakeholder groups. Moreover, many costs and benefits ultimately depend on how individual ranchers, landowners, and resource users respond to changes in risk. Because many of these costs and benefits will not be realized in the short term, a long-term perspective is needed in managing the entire system. Bioeconomic modeling provides a valuable framework for systems-level decision making that is able to take into account the socioeconomic costs and benefits of reducing transmission from wildlife to domestic cattle and bison, and it is able to promote coordination and targeting of actions spatially and temporally based on expected costs and benefits, including potential impacts beyond the GYA. While the Statement of Task requests a cost-benefit analysis for various management options, a lack of critical information severely limits the committee's ability to develop a comprehensive empirical assessment at this time. There are significant knowledge gaps for key economic and disease ecology relations, including the effectiveness, cost, and unanticipated impacts of various candidate management options to control brucellosis in the broader GYA system.

A coupled systems/bioeconomic framework is vital for evaluating the socioeconomic costs and benefits of reducing brucellosis in the GYA and would be needed to weigh the potential costs and benefits of particular management actions within an adaptive management setting. A bioeconomic framework is also needed to identify appropriate management actions to target spatial-temporal risks, including risks beyond the GYA (Conclusion 9).

A Call to Strategic Action

The current committee echoes the sentiments from the 1998 NRC report and concurs that eradication of brucellosis from the GYA remains idealistic but is still not currently feasible for scientific, social, political, and economic reasons. However, while eradication of brucellosis in the GYA remains a distant goal, significant progress toward reducing or eliminating brucellosis transmission from wildlife to domestic species is possible. Undoubtedly, sufficient societal and political will along with sufficient financial resources will be required for success. **Managing an ecosystem as complex as the Greater Yellowstone Ecosystem will require coordination and cooperation from multiple stakeholders and will require expertise across many disciplines to understand the intended and unintended costs and benefits of actions (Conclusion 10).** Addressing brucellosis under the new and changing conditions in the region necessitates a more systematic, rigorous, and coordinated approach at several levels—from priority setting to information gathering, data sharing, and wildlife and disease management—than has occurred thus far. **A strategic plan is needed to coordinate future efforts, fill in critical knowledge and information gaps, and determine the most appropriate management actions under a decision-making framework that is flexible and accounts for risks and costs (Conclusion 11).**

Recommendation 6: All federal, state, and tribal agencies with jurisdiction in wildlife management and in cattle and domestic bison disease control should work in a coordinated, transparent manner to address brucellosis in multiple areas and across multiple jurisdictions. Effectiveness is dependent on political will, a respected leader who can guide the process with goals, timelines, meas-

Revisiting Brucellosis in the Greater Yellowstone Area

ured outcomes, and a sufficient budget for quantifiable success. Therefore, participation of leadership at the highest federal (Secretary) and state (Governor) levels—for initiating and coordinating agency and stakeholder discussions and actions and in sharing information—is critical.

Coordinating a Complex System

Management of brucellosis in the GYA is under the jurisdiction of various state, federal, private, and tribal authorities. Each entity has its own mission and goals, and at times these goals may conflict with one another. In addition, there are private landowners, hunters, and ranchers whose actions can impact and are impacted by the decisions of others. To date, the efforts undertaken by various state and federal entities have been conducted in a piecemeal fashion, resulting in a disjointed and uneven approach. Moreover, actions taken have not been effective in addressing the problem because they have not addressed the issues on a systems level. While each state has the right to establish independent management approaches, management actions within each state can have external impacts for the other two states in the GYA and beyond; similarly, each federal agency has the right to establish independent management approaches for their area of jurisdiction, yet there may be unintended consequences that impact the mission and goals of other agencies. Thus, **coordinated efforts across federal, state, and tribal jurisdictions are needed, recognizing firstly that *B. abortus* in wildlife spreads without regard to political boundaries and secondly that the current spread of brucellosis will have serious future implications if it moves outside of the GYA (Conclusion 12).** Future progress will depend on actions of private and public stakeholders and will require integrating multiple scientific approaches.

Integration of Management Approaches

Historically, there was great interest in brucellosis at the highest levels of government through the Greater Yellowstone Interagency Brucellosis Committee. While the threat has expanded since 1998, the participation of essential stakeholders has diminished due to loss of interest caused by lack of a positive outcome or productive movement in the disease progression within the wildlife populations. There is a need to reinvigorate this interest with buy-in and participation of leadership and development of a mechanism for coordinating policy and management actions.

Integration of Scientific Approaches

Lack of openly accessible data has limited the amount of scientific progress on controlling brucellosis, slowed the learning process, and limited critical information necessary for making decisions. A forum to coordinate scientific approaches toward brucellosis control among all states and agencies with jurisdiction in the GYA would be a valuable mechanism to ensure that science informs policy. Such a body would share information, prioritize research projects, limit duplication of efforts, advise on management actions, and serve as a potential venue for communicating scientifically sound and agreed-upon messages and policies to the public.

Addressing Knowledge Gaps Through Research

Eliminating *B. abortus* transmission within wildlife populations (elk and bison) and from wildlife to cattle and domestic bison in the GYA—and by extension, eliminating it from the United States—is not feasible unless critical knowledge gaps are addressed. An integrated, multidisciplinary approach is necessary for addressing multiple aspects of the problem; thus, research teams will need to include members from various disciplines who provide relevant expertise and understanding. This will also require collaboration and coordinated communications among the university, agency, and nonprofit research communities.

Summary

Recommendation 7: The research community should address the knowledge and data gaps that impede progress in managing or reducing risk of *B. abortus* transmission to cattle and domestic bison from wildlife.

7A: Top priority should be placed on research to better understand brucellosis disease ecology and epidemiology in elk and bison, as such information would be vital in informing management decisions.

7B: To inform elk management decisions, high priority should be given to studies that would provide a better understanding of economic risks and benefits.

7C: Studies and assessments should be conducted to better understand the drivers of land use change and their effects on *B. abortus* transmission risk.

7D: Priority should be given to developing assays for more accurate detection of *B. abortus* infected elk, optimally in a format capable of being performed pen-side to provide reliable rapid results in the field.

7E: Research should be conducted to better understand the infection biology of *B. abortus*.

7F: To aid in the development of an efficacious vaccine for elk, studies should be conducted to understand elk functional genomics regulating immunity to *B. abortus*.

7G: The research community should (1) develop an improved brucellosis vaccine for cattle and bison to protect against infection as well as abortion, and (2) develop a vaccine and vaccine delivery system for elk.

CONCLUDING REMARKS

Even over the course of the committee's 16-month review, there were rapid changes in management practices and new cases of brucellosis in cattle and domestic bison, which re-emphasizes the difficulty in handling this complex and expanding problem. Brucellosis was eliminated from cattle in the United States after nearly a century of dedicated funding and resources from USDA, states, and livestock producers. With increasing incidence of brucellosis in cattle and domestic bison herds in the GYA in the past few decades due to transmission from elk, significant resources are needed to address a problem that is expanding in scale and scope; without the changes and investments necessary to aggressively address this problem in a coordinated and cost-effective manner, brucellosis may spread beyond the GYA into other parts of the United States resulting in serious economic and potential public health consequences. Efforts to reduce brucellosis in the GYA will depend on significant cooperation among federal, state, and tribal entities and private stakeholders as they determine priorities and next steps in moving forward. The report's intent is to be useful for decision makers and stakeholders as they address the challenging matter of brucellosis in the GYA.

1

Introduction

1. BACKGROUND

Brucellosis, a zoonotic bacterial disease, was first noted in the Greater Yellowstone Area (GYA) in 1917 and has been present in the GYA since then. In 1998, the National Research Council (NRC, now referred to as the National Academies of Sciences, Engineering, and Medicine, or “the National Academies”) was asked to review the scientific knowledge regarding *Brucella abortus* transmission among wildlife—particularly bison and elk—and cattle in the GYA (NRC, 1998). That study considered the mechanisms of transmission, risk of infection, and vaccination strategies. It also assessed the infection rate among bison and elk and described what was known about the prevalence of *B. abortus* among other wildlife.

Since that study was conducted, brucellosis has re-emerged in domestic cattle and bison herds in the GYA. From 1990 to 2001, no infected domestic herds were identified. However, between April 2002 and November 2016, 22 beef cattle herds and 5 domestic bison herds were found to be infected. Brucellosis is a nationally and an internationally regulated disease, and the GYA is the last known *B. abortus* reservoir in the United States.

Brucellosis infection and its management have multiple consequences for the local GYA economies (related to livestock and wildlife), and it can potentially affect export of domestic livestock nationally and internationally. In cattle, *B. abortus* infection results in late-gestation abortion, decreased milk production, loss of fertility, and lameness. Placental infection with production of very high numbers of bacteria is the dominant pathologic manifestation associated with transmission. A similar clinical syndrome occurs in bison infected with *B. abortus* (Rhyan et al., 2009). In the United States, brucellosis is no longer a major human health concern (CDC, 2012). However, in less-developed countries, brucellosis in humans resulting from direct exposure to infective material and consumption of unpasteurized milk products is a serious recurring illness; it is consistently one of the most economically important zoonoses globally (McDermott et al., 2013). *Brucella* bacteria have been found in flies (*Musca autumnalis*) associated with cattle and lungworms of seals (Garner et al., 1997); however, no current evidence suggests that these are important vectors of disease transmission.

Brucellosis is endemic in bison and elk in the GYA. The GYA is home to more than 5,500 bison that are the genetic descendants of the original free-ranging bison herds that survived in the early 1900s. Roughly 60% of Yellowstone bison are seropositive for *Brucella* (Hobbs et al., 2015). The GYA is also home to more than 125,000 elk, whose habitats are managed through interagency efforts, including the National Elk Refuge (NER) and 22 supplemental winter feedgrounds maintained in Wyoming. Seroprevalence in feedground elk ranges from about 10% to 40% (Scurlock and Edwards, 2010).

Feedgrounds reduce the seasonal loss of elk in winter, thereby increasing the elk population and changing other elk behaviors, such as those related to parturition. Comingling of elk with cattle is the cause of current brucellosis outbreaks in cattle. Although most cattle in the GYA are vaccinated with *B. abortus* strain RB51, it does not necessarily prevent infection but it does reduce abortions (Olsen, 2000).

Introduction

B. abortus isolates recovered from infected cattle very closely resemble or are indistinguishable from isolates in wild elk. Over the past decade, seroprevalence in some elk herds increased without direct exposure to feedground elk. This finding suggests that brucellosis is now self-sustaining in free-ranging elk distant from the feedgrounds and thus accounts for increased risk to cattle. Other factors that increase the complexity in managing brucellosis and the Greater Yellowstone Ecosystem (GYE) include the 1995 reintroduction and subsequent recovery in numbers of grey wolves in Yellowstone, changes in land use, and changes in federal and state regulations. The GYA is now home to 400-450 wolves (Jimenez and Becker, 2015), which prey primarily on elk. Furthermore, the grizzly bear population has increased, with 150 having home territories in the Park itself (Yellowstone Park, 2016) and approximately 500-600 with ranges in the GYA (USFWS, 2016). These changes have led to movement of elk outside YNP and into areas where increased exposure to cattle can occur.

In 1998, bison were the primary focus of the NRC's evaluation of brucellosis in the GYA. Since that time, the Interagency Bison Management Plan (IBMP) was implemented to achieve the spatial separation of bison and cattle, which has dramatically reduced the risk of bison transmitting *B. abortus* to cattle. Bison remain an important focus, but it is clearly evident that the rate of transmission from elk has increased significantly. The GYA is a complex and dynamic ecosystem that requires both a reanalysis of changed and changing factors and recommendations on strategies and goals in light of those factors.

2. THE GREATER YELLOWSTONE AREA

The GYA (see Figure 1-1) has been defined as the general area including and surrounding Yellowstone and Grand Teton National Parks, spanning about 400 km north-to-south and 200 km east-to-west (White et al., 2015). The general boundaries of the GYA were delimited by the Greater Yellowstone Coordinating Committee in 1994 (McIntyre and Ellis, 2011). The GYA consists of Yellowstone and Grand Teton National Parks as core natural areas that are surrounded by six national forests, three national wildlife refuges, state lands, Bureau of Land Management (BLM) land parcels, and private and tribal lands (White et al., 2015). These areas are administered by many different federal and state management entities. The federal agencies responsible for overseeing those lands include the National Park Service (NPS), the U.S. Fish & Wildlife Service (USFWS), BLM—which are part of the U.S. Department of the Interior (DOI)—and the U.S. Department of Agriculture's (USDA's) Forest Service (USFS). The state agencies include Idaho Department of Fish and Game, Idaho State Department of Agriculture, Montana Department of Fish, Wildlife & Parks (MDFWP), Montana Department of Livestock, Wyoming Game & Fish Department (WGFD), and Wyoming Livestock Board.

2.1 Terminology

The GYA is included within an area that has been referred to as the GYE, one of the largest, mostly intact, temperate ecosystems in the world (Keiter and Boyce, 1991). The GYE was originally defined as the range of the Yellowstone grizzly bear (Craighead, 1991; Gude et al., 2006), but ecosystem boundaries are somewhat subjective and dependent on movements and interactions among many species. For the purposes of this report, the area of interest includes the GYA, but also areas in and near the GYA where brucellosis is known to occur in elk and bison and where there is a risk of transmission to domestic livestock and domestic bison herds (see Figure 1-2). Areas with brucellosis presence or risk of transmission are included in the brucellosis designated surveillance areas (DSAs) of eastern Idaho, southwest Montana, and western Wyoming.

Revisiting Brucellosis in the Greater Yellowstone Area

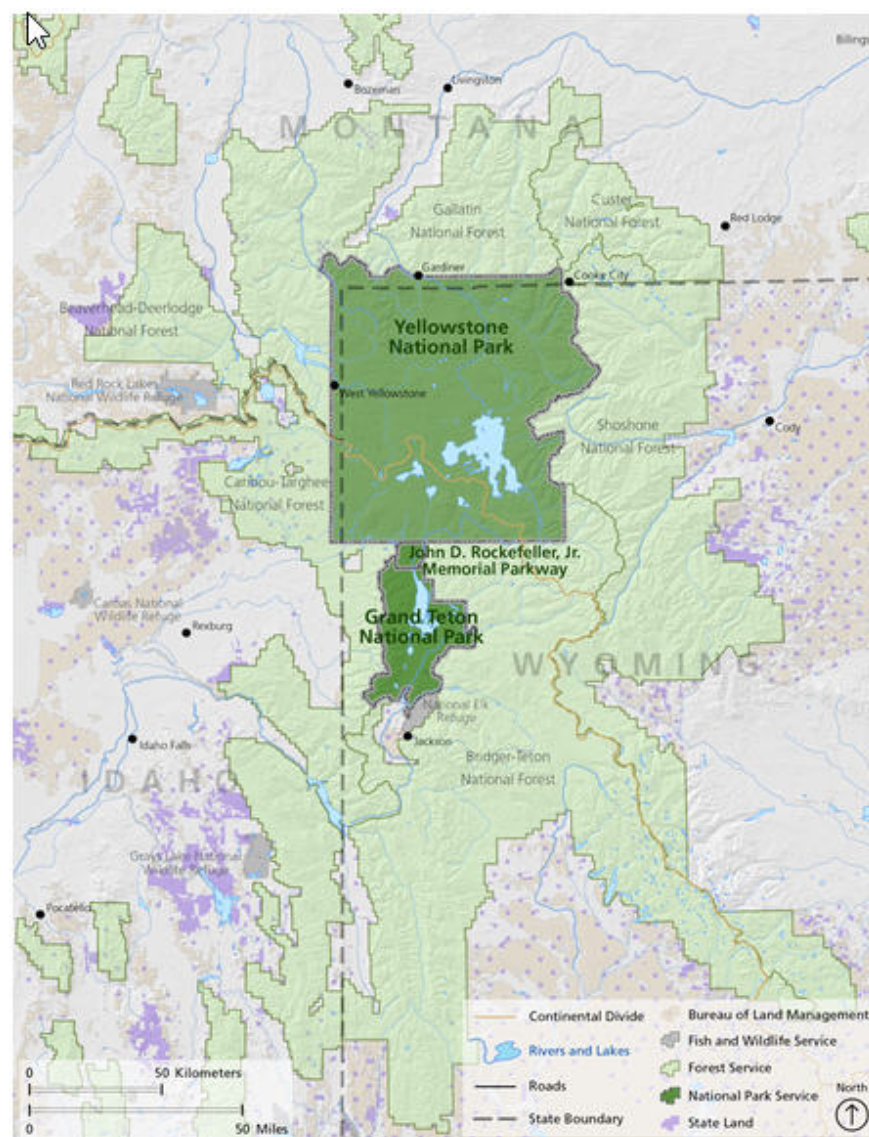


FIGURE 1-1 Map of the GYA by jurisdiction. SOURCE: NPS, 2016.

2.2 Bison and Elk Populations

As of 2016, the GYA supports more than 5,500 bison. The great majority are found in the YNP herd, which varies in size between 3,000 and 6,000 animals. Since 1998, when the previous NRC brucellosis report was written, the YNP bison population has increased from 3,000-4,000 to 4,000-5,000. YNP bison are primarily found within the Park boundaries, but they also use areas outside of the Park to the north and west. The YNP herd consists of two subherds, central and northern, with some interchange between them. In contrast to 1998, when there were considerably more bison in the central herd than in the northern herd, there are now more bison in the northern herd. A second and much smaller herd of about 700 bison has a core range inside Grand Teton National Park (GTNP), with most wintering on the NER (Koshmrl, 2015).

Introduction

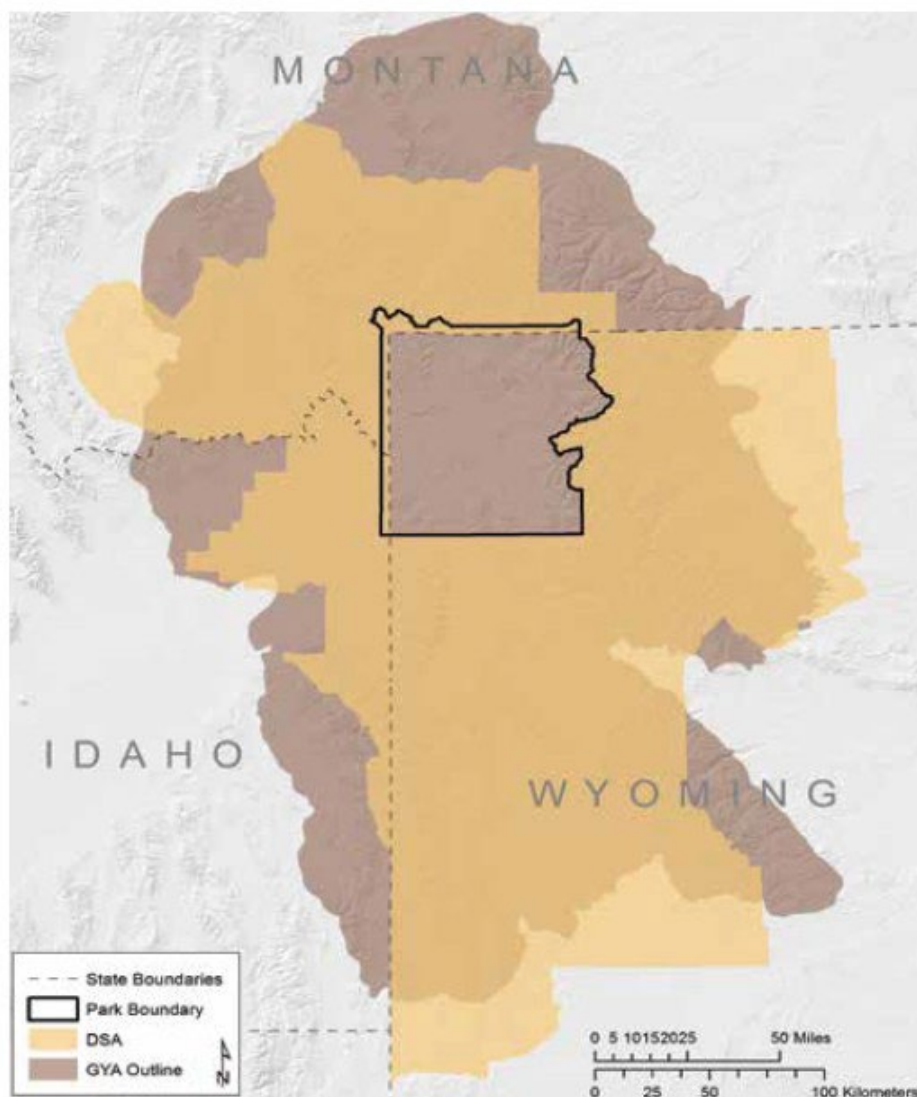


FIGURE 1-2 Map showing GYA boundary and designated surveillance areas as of 2016. SOURCE: White et al., 2015.

There are more than 125,000 elk in the GYA. Several herds have winter ranges in and around YNP, including the northern Yellowstone winter range herd, which was, up until recently, the largest herd in the GYA. A second set of herds, the Jackson herds, have winter ranges in the southern parts of the GYA, including the USFWS NER and surrounding areas near the town of Jackson. The Jackson herd has been larger than the northern Yellowstone herd for the past two decades. Within YNP, elk have been managed by NPS under a policy of natural regulation, in which it is hypothesized that the area is large enough for populations to be regulated by food limitation or predation, without a need for artificial reductions. However, YNP elk ranges extend beyond park boundaries. Elk outside YNP are managed by state and federal wildlife management agencies. YNP provides summer range for six to seven elk herds, most of which spend the winter at lower elevations outside YNP (NPS, 2015).

*Revisiting Brucellosis in the Greater Yellowstone Area***3. ADMINISTRATIVE COMPLEXITY OF THE GREATER YELLOWSTONE AREA****3.1 Regulatory Authority of Various Species**

Cattle, bison, and elk are managed by different state and federal agencies. For cattle, USDA's Animal and Plant Health Inspection Service (USDA-APHIS) has regulatory oversight of livestock, with objectives to safeguard livestock health, maintain the economic viability and trade capabilities of the U.S. cattle industry, and protect public health and food safety (Clarke, 2015). USDA-APHIS has the national authority to suppress and prevent the spread of any contagious and infectious disease of livestock, which could include establishing quarantines, regulating the movement of livestock, and seizing and disposing of livestock (Clarke, 2015). Similarly, state departments of agriculture or their equivalent have regulatory oversight of livestock and are responsible for protecting producers, trading partners, and public health in their respective states.

Bison and elk move across wide ranges of land and, not surprisingly, their management crosses administrative boundaries. The NPS has jurisdiction in managing bison within Yellowstone and Grand Teton National Parks. Outside the national parks, bison are under the authority of state agencies and may be considered as either wildlife or livestock, depending on the context. In Wyoming, bison are considered wildlife in specific designated areas adjacent to Yellowstone and Grand Teton National Parks (Becker et al., 2013). In Montana, the Yellowstone bison population is considered as wildlife, with MDFWP managing hunting on lands adjacent to YNP and with the Montana Department of Livestock in charge of disease control management (Becker et al., 2013). For the purpose of brucellosis management, USDA considers all bison removed from YNP as alternate livestock (Becker et al., 2013). Only in the event of a national disease emergency would USDA-APHIS have authority over wildlife.

For elk, DOI has jurisdiction inside Yellowstone and Grand Teton National Parks, the USFS is responsible for providing habitat on national forest lands, the BLM has authority over its land parcels, and the USFWS (DOI) manages the NER. With regard to the states, the state wildlife management agencies in Idaho, Montana, and Wyoming have authority over elk population management anywhere outside of the national parks.

In addition to the state and federal agencies, there are three Native American Indian reservations in the near vicinity of the DSA: Fort Hall, Wind River, and Crow. The Fort Hall Reservation of the Shoshone-Bannock Tribes is in southeastern Idaho (over 2,000 km²). The Wind River Reservation created for the Eastern Shoshone and Northern Arapaho Tribes is approximately 9,000 km² and is located on the eastern side of the Wind River mountains in Wyoming. Wild bison were recently translocated into the Wind River Reservation in 2016. The Crow Indian Reservation for the Crow Tribe is located in Montana north of the Bighorn Mountains (9,300 km²).

3.2 Coordination and Management of Bison and Elk Among Agencies

Yellowstone elk populations migrate, disperse, and utilize habitats outside of the national parks and are managed by state wildlife authorities for recreational hunting. This means that despite any policy of natural regulation or ecosystem process management of the NPS, elk populations that spend a part of the year inside Yellowstone and Grand Teton National Parks can be and are managed by state game management agencies through hunter harvests, to varying degrees. The extent to which hunting controls elk populations relative to habitat and food limitation and winter weather inside YNP and GTNP has been insufficiently recognized or characterized. Clearly a major goal of state wildlife authorities is to produce thriving and sustainable populations of wildlife, primarily for hunting and fishing. However, state wildlife authorities also serve multiple stakeholders. For example, MDFWP manages Montana's fish and wildlife populations and habitats while balancing the interests of groups such as hunters, outdoor recreationists, visitors, landowners, and the general public (MDFWP, 2004). Consistent with the mission of the National Wildlife Refuge System in sustaining healthy wildlife populations (USFWS and NPS, 2007), the mission of the

Introduction

USFWS's NER is to "contribute to elk and bison populations that are healthy and able to adapt to changing conditions in the environment and that are at reduced risk from the adverse effect of non-endemic diseases."

The need for coordination among agencies in managing bison and elk led to the formation of numerous coordinated management plans such as the IBMP (2014) and the Bison and Elk Management Plan for the NER and GTNP (USFWS and NPS, 2007). It also led to numerous interagency working groups and committees, such as the Northern Yellowstone Cooperative Wildlife Working Group (which coordinates management of the northern Yellowstone elk herd) (Cross, 2013); the Jackson Interagency Habitat Initiative; and the Greater Yellowstone Interagency Brucellosis Committee (which is no longer operational). Similar GYA-scale efforts have been organized for grizzly bears (Interagency Grizzly Bear Study Team) and for wolves (Northern Rocky Mountain Wolf Recovery Program; Jimenez and Becker, 2015).

4. PURPOSE OF THIS STUDY

USDA-APHIS requested that the National Academies revisit the issue of brucellosis in the GYA. The primary motivation for USDA-APHIS was to understand the factors associated with the increased occurrence of brucellosis transmission from wildlife to livestock; the recent apparent expansion of brucellosis in non-feedground elk; and the desire to have science inform the future course of any actions used to address brucellosis in the GYA. Although USDA-APHIS commissioned the study to inform its brucellosis eradication strategy, the GYA comprises some 145,000 km², including state, federal (BLM), private, and tribal lands, as well as national parks, forests, and wildlife refuges. Each political entity has its own mission and goals, including disease management, ecosystem management, and recreational purposes. This subject is of great interest to many people of widely divergent backgrounds and experience, and public opinion also needs to be accounted for because YNP is a national icon. Therefore, a broader audience for the report is addressed apart from USDA-APHIS, including other federal agencies such as the NPS and the USFS, state and tribal governments, and the public, both nationally and locally, including hunters and ranchers with economic interests in wildlife and domestic food animals in the GYA. The Statement of Task for the study attempts to address those concerns and encompass the complexity of the issues (see Box 1-1).

5. APPROACH TO THE TASK

The National Academies convened a committee of 11 experts who collectively have extensive experience in veterinary pathology, wildlife biology, molecular immunology, vaccinology, laboratory diagnostics, brucellosis regulatory program management, disease modeling, ecology, and agricultural and natural resource economics. (See Appendix A for the committee membership and biographies.) Using the 1998 report as a launching point for the current report, the committee conducted an extensive scientific literature review to inform its current understanding of brucellosis.

The committee held three meetings as part of the information-gathering process.¹ (See Appendix B for the open session meeting agendas.) The committee solicited information from multiple sources, including the sponsor (USDA-APHIS), NPS, USFS, and the state governments of Idaho, Montana, and Wyoming. To augment its understanding of the GYA, the committee participated in a field trip through YNP hosted by the NPS. The committee also gathered information from researchers who have contributed to the scientific body of work on brucellosis. At each of these meetings, members of the public provided comments that informed the committee in addressing its task.

¹As part of the information-gathering process, materials submitted to the committee (presentations and written materials) by external sources are listed in the project's public access file and can be made available to the public upon request by contacting the Public Access Records Office at paro@nas.edu.

*Revisiting Brucellosis in the Greater Yellowstone Area***BOX 1-1 Statement of Task**

In an update of the National Research Council (NRC) report *Brucellosis in the Greater Yellowstone Area* (1998), an NRC-appointed committee will comprehensively review and evaluate the available scientific literature and other information on the prevalence and spread of *Brucella abortus* in the Greater Yellowstone Area (GYA) in wild and domestic animals and examine the feasibility, time-frame, and cost-effectiveness of options to contain or suppress brucellosis across the region.

The study will examine factors associated with the increased occurrence of brucellosis transmission from wildlife to livestock and the recent expansion of brucellosis in non-feedground elk, including whether evidence suggests that brucellosis is self-sustaining in elk or if reinfection through emigration from feeding grounds is occurring. The study also will explore the role of feeding grounds, predators, population size and other factors in facilitating brucellosis infection.

The study committee will examine disease management activities and vaccination strategies being undertaken or considered at the state, regional, and federal level, and evaluate the biological, animal health, and public health effects of those activities. The committee also will examine the current state of brucellosis vaccines, vaccine delivery systems, and vaccines under development for bison, cattle, and elk, as well as the effectiveness of currently available vaccination protocols. In the course of its review, the committee will explore the likelihood of developing more effective vaccines, delivery systems, and diagnostic protocols for cattle, bison and elk.

Throughout the study, the committee will meet with wildlife managers, animal health officials, land managers, native peoples, and other stakeholders, including the members of the public, to understand the implications of brucellosis control efforts on other goals and activities in the region and nationally. The committee will examine the societal and economic costs and benefits of implementing various measures to reduce or eliminate the risk of brucellosis transmission to cattle and within wildlife relative to the costs and benefits of allowing the persistence of brucellosis in the GYA.

In a consensus report, the committee will summarize the findings and conclusions of its analysis and based on the scientific evidence, describe the likely effectiveness and trade-offs of options that could be used to address brucellosis in the GYA. In addition, the report will describe and prioritize further research needed to reduce uncertainties and advance the knowledge base on brucellosis vaccines, vaccine delivery mechanisms, and diagnostics.

6. ORGANIZATION OF THE REPORT

The remainder of the report is divided into three sections: an overview of the current situation and a review of new information since the previous 1998 report (Chapters 2-5); an examination of integrative adaptive management approaches and tools for addressing brucellosis (Chapters 6-8); and a look at future research needed to address brucellosis in the GYA (Chapter 9). In describing recent developments since the 1998 report, Chapter 2 examines the geographic scope of bison and elk populations across the GYA, and discusses the implications of land use changes and changing climate for bison and elk populations. Chapter 3 discusses the prevalence and epidemiology of *B. abortus* in the GYA. Chapter 4 provides an overview of the current scientific understanding of *B. abortus* and discusses how new scientific tools have been critical in contributing to the body of knowledge for understanding brucellosis transmission, pathogenesis, and risk management. The management efforts of federal, state, and regional partners are discussed in Chapter 5. Chapter 6 describes integrative adaptive management approaches to be adopted as part of a strategy for addressing brucellosis in the GYA, and Chapter 7 outlines management options for managing brucellosis. Bioeconomic analysis of wildlife diseases management has emerged as a new research area since the 1998 report, and the use of a bioeconomic framework that can address economic and social aspects of the issues (discussed in Chapter 8) will be critical for making decisions. Chapter 9 outlines some remaining research gaps to understanding and controlling brucellosis in the GYA. The last chapter of the report (Chapter 10) synthesizes the concerns and provides the committee's overall findings, conclusions, and recommendations related to its Statement of Task.

Introduction

REFERENCES

- Becker, M.S., R.A. Garrott, and P.J. White. 2013. Scale and perception in resource management: Integrating scientific knowledge. Pp. 29-46 in *Yellowstone's Wildlife in Transition*. P.J. White, R.A. Garrott, and G.E. Plumb, eds. Cambridge, MA: Harvard University Press.
- CDC (Centers for Disease Control and Prevention). 2012. Brucellosis Surveillance: National Notifiable Disease Surveillance System, 1993-2010. Available online at <http://www.cdc.gov/brucellosis/resources/surveillance.html> (accessed May 17, 2016).
- Clarke, P.R. 2015. USDA Regulatory Oversight of Brucellosis (*Brucella abortus*). Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 1-2, 2015, Bozeman, MT.
- Craighead, J.J. 1991. Yellowstone in transition. Pp. 27-40 in *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage*. R.B. Keiter and M.S. Boyce, eds. New Haven, CT: Yale University Press.
- Cross, P. 2013. Northern Yellowstone Cooperative Wildlife Working Group 2012 Annual Report. Available online at <http://www.fedgycc.org/wp-content/uploads/2015/06/2012NYCW WGfNlRpt.pdf> (accessed January 4, 2017).
- Garner, M.M., D.M. Lambourn, S.J. Jeffries, P.B. Hall, J.C. Rhyhan, D.R. Ewalt, L.M. Polzin, and N.F. Cheville. 1997. Evidence of *Brucella* Infection in Parafilaroides Lungworms in a Pacific Harbor Seal (*Phoca Vitulina Richardsi*). *Journal of Veterinary Diagnostic Investigation* 9(3):298-303.
- Gude, P.H., A.J. Hansen, R. Rasker, and B. Maxwell. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. *Landscape Urban Planning* 77:131-151.
- Hobbs, N.T., C. Geremia, J. Treanor, R. Wallen, P.J. White, M.B. Hooten, and J.C. Rhyhan. 2015. State-space modeling to support management of brucellosis in the Yellowstone bison population. *Ecological Monographs* 85(4):525-556.
- IBMP (Interagency Bison Management Plan). 2014. IBMP Adaptive Management. National Park Service, USDA-Forest Service, USDA-Animal & Plant Health Inspection Service, Montana Department of Livestock and Montana Fish, Wildlife & Parks. Available online at <http://www.ibmp.info/adaptivemgmt.php> (accessed January 4, 2017).
- Jimenez, M.D., and S.A. Becker, eds. 2015. Northern Rocky Mountain Wolf Recovery Program 2014 Interagency Annual Report. U.S. Fish & Wildlife Service, Idaho Department of Fish and Game, Montana Fish, Wildlife & Parks, Wyoming Game & Fish Department, Nez Perce Tribe, National Park Service, Blackfeet Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. Helena, MT: USFWS, Ecological Services.
- Keiter, R.B., and M.S. Boyce. 1991. *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage*. New Haven, CT: Yale University Press. 428 pp.
- Koshmrl, M. 2015. Jackson bison numbers are down, as planned. *Jackson Hole Daily*. March 10. Available online at http://www.jhnewsandguide.com/news/environmental/jackson-bison-numbers-are-down-as-planned/article_ed378467-2cae-5a23-b7ab-b7185e1731a4.html (accessed January 12, 2017).
- McDermott, J., D. Grace, and J. Zinsstag. 2013. Economics of brucellosis impact and control in low-income countries. *Revue scientifique et technique International Office of Epizootics* 32(1):249-261.
- McIntyre, C., and C. Ellis. 2011. Landscape Dynamics in the Greater Yellowstone Area. Natural Resource Technical Report NPS/GRYN/NRTR-2011/506. Fort Collins, CO: National Park Service, U.S. Department of the Interior.
- MDFWP (Montana Department of Fish, Wildlife & Parks). 2004. Montana Statewide Elk Management Plan. Helena, MT: Montana Department of Fish, Wildlife & Parks.
- NPS (National Park Service). 2015. Yellowstone Resources and Issues 2015. Available online at <http://www.nps.gov/yell/learn/resources-and-issues.htm> (accessed May 25, 2016).
- NPS. 2016. Map of the Greater Yellowstone Area. Available online at <https://www.nps.gov/yell/learn/nature/greateryellowstonemap.htm> (accessed May 25, 2016).
- NRC (National Research Council). 1998. *Brucellosis in the Greater Yellowstone Area*. Washington, DC: National Academy Press.
- Olsen, S.C. 2000. Immune Responses and Efficacy after Administration of a Commercial *Brucella abortus* Strain RB51 Vaccine to Cattle. *Veterinary Therapeutics* 1(3):183-191.
- Rhyhan, J.C., K. Aune, T. Roffe, D. Ewalt, S. Hennager, T. Gidlewski, S. Olsen, and R. Clarke. 2009. Pathogenesis and epidemiology of brucellosis in yellowstone bison: Serologic and culture results from adult females and their progeny. *Journal of Wildlife Diseases* 45(3):729-739.

Revisiting Brucellosis in the Greater Yellowstone Area

- USFWS (U.S. Fish & Wildlife Service). 2016. Draft 2016 Conservation Strategy for the Grizzly Bear in the Great Yellowstone Ecosystem. Missoula, MT. Available online at [https://www.fws.gov/mountain-prairie/es/grizzly Bear.php](https://www.fws.gov/mountain-prairie/es/grizzly-bear.php) (accessed May 16, 2016).
- USFWS and NPS. 2007. Bison and Elk Management Plan for the National Elk Refuge and Grand Teton National Park. Available online at <http://www.fws.gov/bisonandelkplan> (accessed January 4, 2017).
- White, P.J., R.L. Wallen, and D.E. Hallac. 2015. *Yellowstone Bison Conserving an Icon in Modern Society*. Yellowstone National Park, WY: Yellowstone Association.
- Yellowstone Park. 2016. Yellowstone Grizzly Bears by the Numbers. Available online at <http://www.yellowstonepark.com/grizzly-bear-facts> (accessed May 16, 2016).

2

Geographic Scope of Populations and Disease and Change in Land Use

1. INTRODUCTION

There have been significant changes in the population sizes and distributions of bison and elk in the Greater Yellowstone Area (GYA) since the 1998 National Research Council report. Both bison and elk numbers have increased overall. Bison ranges have expanded and there is increased intermixing among herds. Elk numbers have increased in many areas, while the population size of the well-known Yellowstone northern range herd has declined. Elk are now recognized as a large reservoir of *B. abortus*. In addition, wolves were reintroduced to the GYA and grizzly bear numbers have increased. As a result of all these changes, brucellosis transmission dynamics are considerably different than in 1998.

The changes in *B. abortus* reservoir and transmission dynamics in the GYA are also outcomes of processes associated with the ecologies, population dynamics, and spatial distributions of bison and elk. Bison and elk also play critical roles in the functioning of the Greater Yellowstone Ecosystem as a whole. They affect and also respond to vegetation, soils, other wildlife populations, and human activities.

This chapter examines the ecological context of brucellosis in the GYA as affected by the abundances and spatial distributions of its host species: elk and bison. It draws on best available data to provide a quantitative basis for understanding the abundances and spatial distributions of the two main host species, and it explores factors (such as climate, predators, land use, hunting, changes in management activities) that cause host abundances and distributions to change.

2. ELK POPULATIONS AND DISTRIBUTIONS

One of the most significant changes since 1998 is an increased recognition of the central role that elk play in *B. abortus* transmission. An increase in elk numbers across the GYA is one factor contributing to a change in the role of elk, with more than 125,000 counted elk distributed among 11 major herds. The ranges and migration pathways of 9 of these major herds are shown in Figure 2-1.

Dynamics of the northern Yellowstone elk population have been intensively studied for decades (Houston, 1982; Coughenour and Singer, 1996; Singer et al., 1997; Taper and Gogan, 2002; Barmore, 2003; White and Garrott, 2005a,b; Varley and Boyce, 2006; Eberhart et al., 2007). In 1969, a policy of natural regulation ended artificial reductions that enabled the elk population to swell to its highest levels in the 1980s with more than 18,000 counted elk (Coughenour and Singer, 1996) (see Figure 2-2). In the late 1990s, the population steadily declined following wolf reintroduction, with the 2016 population count at less than 5,000 elk. In modeling and predicting elk population equilibrium levels in the GYA pre-wolves, there was general agreement that food limitation would result in an equilibrium number of approximately 15,000-18,000 counted elk on the northern range, which corresponds to approximately 20,000-24,000 actual elk in the absence of wolves (Coughenour and Singer, 1996; Taper and Gogan, 2002; Coughenour, 2005; Varley and Boyce, 2006).

Revisiting Brucellosis in the Greater Yellowstone Area

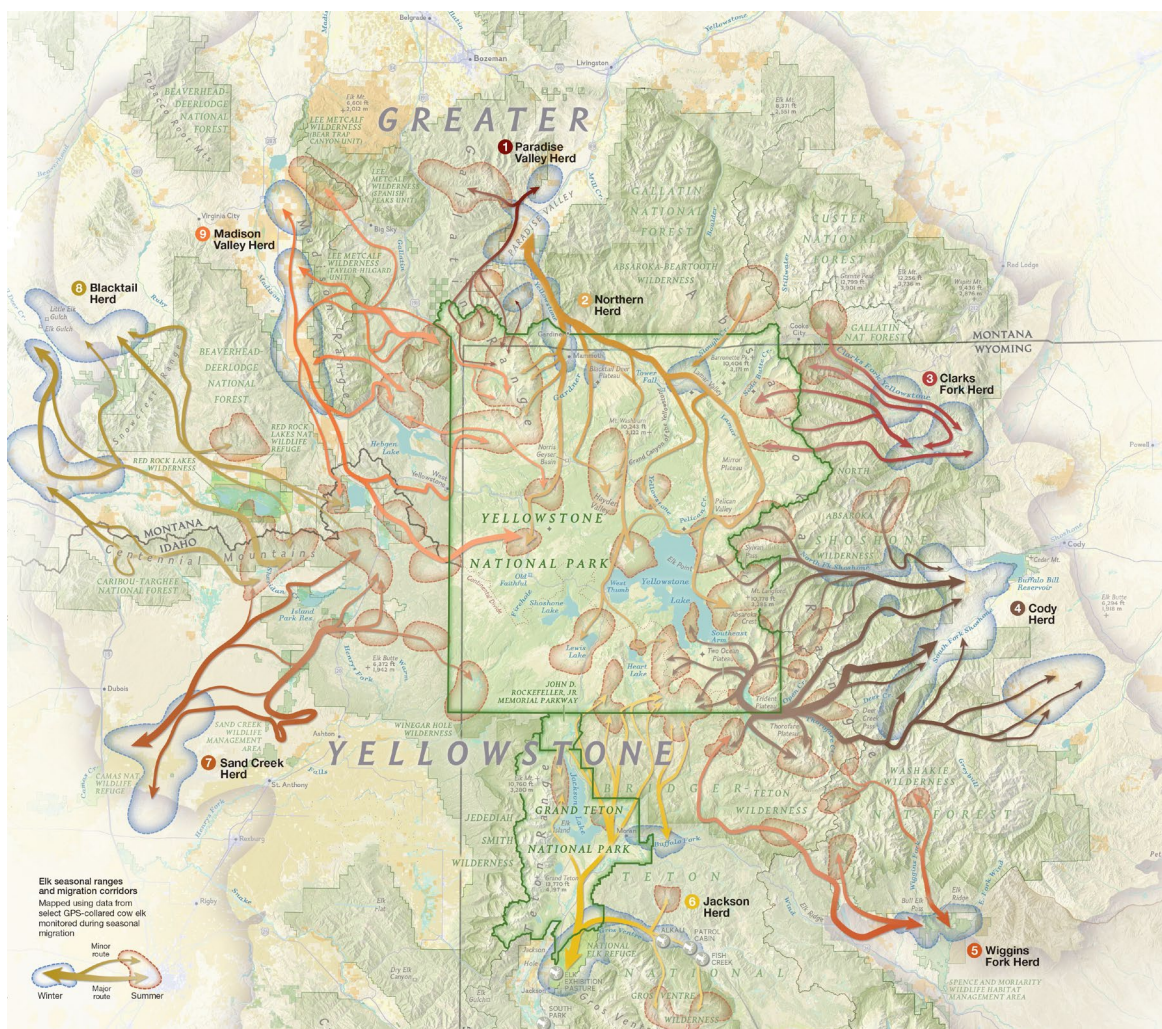


FIGURE 2-1 Map of migration corridors, winter ranges (blue polygons) and summer ranges (tan polygons) of 9 of 11 major elk herds in the GYA. This map excludes approximately one-third of the southern GYA that includes elk in the Afton-Pine, the Pinedale-South Wind River areas, and eastern Idaho, west of Grand Teton National Park (see Figure 2-4 and Tables 2-3 and 2-4). SOURCE: National Geographic, 2016.

2.1 Wolves and Hunting

The beginning of the decline in northern range elk numbers coincided with the reintroduction of wolves in 1995 and 1996, suggesting that wolves were, at least in part, responsible. However, other factors are also probably playing a role, including a high hunting removal of elk migrating north of Yellowstone National Park (YNP), and the fact that hunting harvests have been mostly of prime-aged female elk with high reproductive value (Eberhart et al., 2007). Wolf predation now exceeds hunter harvest, but it has a smaller effect on elk population dynamics because wolves concentrate on calves and older females with less reproductive value (White et al., 2003; Smith et al., 2004; White and Garrott, 2005a; Evans et al., 2006; Wright et al., 2006; Eberhart et al., 2007). Early empirical models of the effects of climate, harvest, and wolves on this elk population indicated that population responses to wolf predation were compensatory, meaning that predators mainly removed animals that would die of other causes anyway (Vucetich et al., 2005). Additionally, there were several consecutive years of drought during 2000-2006, which could have reduced forage and consequently affected elk (MacNulty, 2015). Elk starvation was documented in late

Geographic Scope of Populations and Disease and Change in Land Use

winter 2003-2004, which was mild but preceded by several years of low annual precipitation (Vucetich et al., 2005). Also, grizzly bears—which are major predators on elk, particularly elk calves—doubled to tripled in number between the mid-1980s and mid-2000s (Singer et al., 1997; Harris et al., 2007; Barber-Meyer et al., 2008; Haroldson, 2008; Schwartz et al., 2009; USFWS, 2016).

2.2 Causes of Changes in Elk Spatial Distributions

Wolves also shift elk distributions, as wolves reduce the availability of habitat and total forage. As a result, a greater number of elk are now found at lower elevations outside of YNP where wolves are less abundant (White et al., 2012). Elk are less likely to occupy areas with deeper snow or other conditions that increase predation risk in the presence of wolves (Mao et al., 2005; White et al., 2009, 2013). Thus, wolves may also have contributed to the decline in the northern Yellowstone elk herd indirectly, through a contraction of the elk range and associated forage. The numbers (see Figure 2-3 [top]) and proportions (see Figure 2-3 [bottom]) of elk herds using habitats north of YNP increased markedly during the mid- and late 1970s in response to increased population size, changes in the timing of elk hunts, and protection of winter ranges outside of YNP (Coughenour and Singer, 1996). The proportion of Yellowstone elk north of YNP in winter increased steadily through 2011 and has remained high during 2011-2015 (see Figure 2-3). The increased percentage is due to the decrease in total population size rather than an increase in numbers outside YNP.

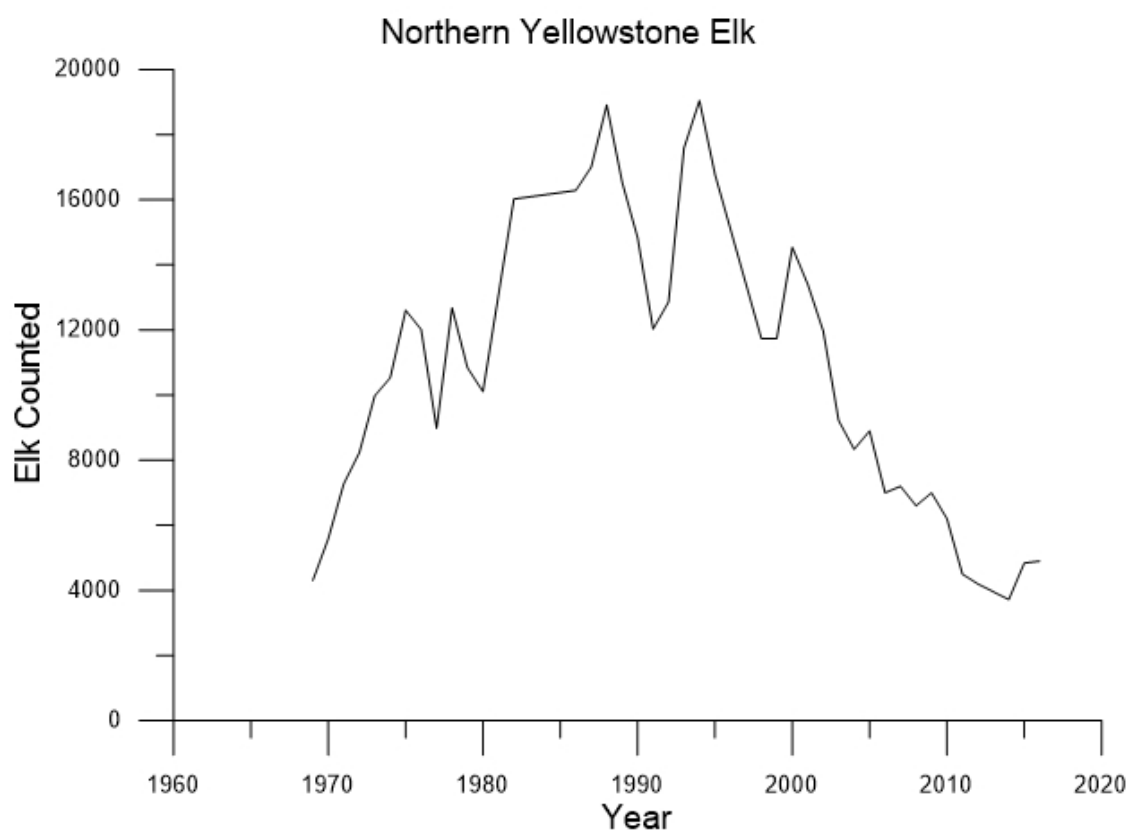


FIGURE 2-2 Northern Yellowstone elk numbers. SOURCES: Coughenour and Singer, 1996; Taper and Gogan, 2002; White and Garrott, 2005a; Cross, 2013.

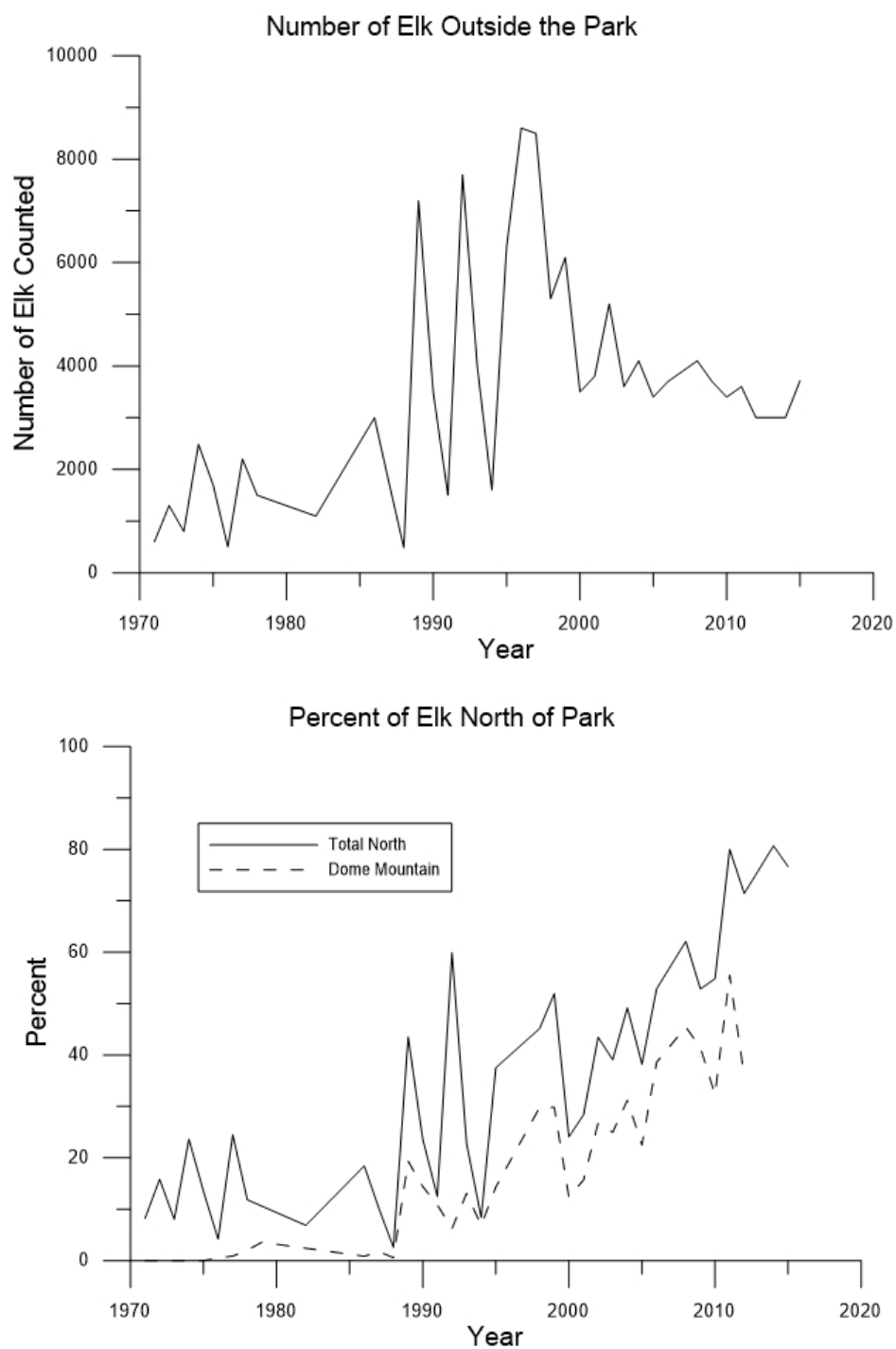
Revisiting Brucellosis in the Greater Yellowstone Area

FIGURE 2-3 Elk numbers and percentages north of YNP and on Dome Mountain. SOURCES: Coughenour and Singer, 1996; Taper and Gogan, 2002; White and Garrott, 2005a; Cross, 2013.

Elk grouping behavior has also changed, as northern Yellowstone elk have been found in larger groups following wolf reintroduction (Mao et al., 2005). Although there was an increase in large groups found outside YNP, there was a decrease in large groups found inside YNP where the elk population has declined (White et al., 2012).

Geographic Scope of Populations and Disease and Change in Land Use

The decline in elk numbers on the northern winter range and the increased proportions of the herd wintering outside YNP could also be due in part to increased competition for forage from increasing numbers of bison. Unlike elk, which migrate to higher elevations in summer, bison remain on the low elevation elk winter range during summer, thereby depleting forage for wintering elk. Ecosystem modeling experiments indicate greater numbers of bison could reduce elk numbers due to dietary and habitat overlaps, but not to the extent to which elk numbers have actually declined (Coughenour, 1994).

2.3 Madison Headwaters Herd

The small herd of elk that resides in the Madison River headwaters within YNP is nonmigratory. This herd spends both winters and summers within YNP and is not subjected to human hunting (Garrott et al., 2003, 2009). The population has declined markedly from approximately 600 in 2001 to about 100 in 2009, likely due to wolves and grizzly bears (Hamlin and Cunningham, 2009). Multiple wolf packs became established by 2002 with a total of 30-40 animals. High wolf densities and moderate elk densities resulted in 20% of elk being taken by wolves (Garrott et al., 2005). Grizzly bear numbers increased from about 10 in the mid-1980s to more than 20 by 2004 (Haroldson, 2006, 2007; Hamlin and Cunningham, 2009). The ratio of grizzly bears to elk was higher in the Madison-Firehole and Gallatin Canyon areas than any other areas across the GYA (Hamlin and Cunningham, 2009).

2.4 Elk Herds Wintering North and West of YNP

Approximately 30,000 elk in elk management units (EMUs) are located north and west of YNP within the brucellosis designated surveillance area (DSA) (see Table 2-1 and Figure 2-4). Approximately 56% of 22 core winter ranges are privately owned, and 10 of the winter ranges in this area have higher than 80% private ownership (personal communication, Quentin Kujala, Montana Department of Fish, Wildlife & Parks [MDFWP], October 30, 2015). Elk numbers in EMUs north and west of YNP in Montana have been increasing since the late 1970s (Cross et al., 2010a), as they have been in many parts of Montana (MDFWP, 2004). In 2008, there were five to nine times more elk in EMUs in the western Paradise and eastern Madison River Valleys of Montana than in 1975. Elk numbers have also been increasing in EMUs just to the north and northwest of the DSA (see Figure 2-5). These include the Bridger, Crazy Mountain, Pioneer, Tandy, and Tobacco Root EMUs.

Elk group sizes have also been increasing, and group size distributions have been increasing in the eastern Madison River and western Paradise Valleys (Cross et al., 2010b). From 2003-2009, there were more large groups and larger group sizes in the northern YNP herd wintering outside YNP than from 1987-1992 (White et al., 2012). In the Madison drainage, elk aggregated in somewhat larger groups in response to wolf predation risk (White et al., 2009). Recently, a pattern was observed of increasing group sizes with increasing density across 27 herd units in this region, and there was no evidence that wolf predation risk affected elk aggregation patterns (Proffitt et al., 2015).

Changes in land ownership have also affected elk migration and aggregation patterns in this region, which have in turn affected hunter access. In the Madison-Gallatin EMU, MDFWP reported that “There is limited access to public land and adjacent private land in some portions of the EMU due to changes in land ownership. This has resulted from a change in land ownership toward landowners who do not make their primary living from ranching” (MDFWP, 2004). Elk migrating from YNP to winter in portions of this EMU, in combination with non-YNP elk, results in high numbers of elk which makes it difficult to control numbers through late-season hunting (MDFWP, 2004). Likewise in the Absaroka EMU, MDFWP further reports, “There has been an increasing number of landowners who do not make their primary living from ranching, and these landowners have less interest than traditional landowners in allowing elk hunting [on their property]” (MDFWP, 2004). As a result, this has created elk refugia, reduced elk harvest, and increased elk numbers. Counts in this EMU are far above management objectives (see Table 2-1).

*Revisiting Brucellosis in the Greater Yellowstone Area***TABLE 2-1** Elk Numbers in EMUs (Hunting Districts) North and Northwest of YNP, But Within the Brucellosis DSA, in 2015

Hunting District	Count 2015	Objective
<i>Northern Yellowstone</i>		
313	3,714	4,000
<i>Absaroka</i>		
317	934	900
520	1,922	1,050
560	2,018	700
Total	4,874	2,650
<i>Gallatin/Madison</i>		
301, 309	587	500
310	428	1,500
311	2,069	2,500
314	3,381	3,000
360 South	773	1,000
360 North	865	1,200
361	—	150
362	2,500	2,952
Total	10,603	12,802
<i>Gravelly</i>		
322-327, 330	10,543	8,000
All Elk Management Units		
Total	29,734	27,452

SOURCE: MDFWP, 2016.

Elk avoidance of hunted areas has resulted in elk groups being unavailable for harvest in the Madison River Valley, which is winter range for approximately 5,000 elk (Proffitt et al., 2010a). During the hunting season, elk shifted to areas that were closed to hunting, including privately owned lands and a state Wildlife Management Area (Wall Creek). The probability of finding elk on such designated refuge areas has more than doubled, with Global Positioning System (GPS)-collared elk in the Madison River Valley showing preference for areas that were privately owned because they faced south and had steeper slopes, lower road densities, and more green forage (Proffitt et al., 2010b). Elk selection for private lands with green forage increases the probability of overlap with cattle and increases the risk of disease transmission.

2.5 Elk Herds Wintering East and South of YNP Boundaries

The Clarks Fork Herd East of YNP

The Clarks Fork elk herd consists of about 4,500 migratory and nonmigratory elk that inhabit the Absaroka Mountains northeast of YNP (Middleton et al., 2013a,b). The winter range of the migratory herd segment includes areas east of YNP, extending to the foothills northwest of Cody. In the spring, the migrants move 40-60 km to high elevation summer ranges inside YNP (Middleton et al., 2013a). The resident herd segment spends winters and summers northwest of Cody, overlapping a portion of the migratory winter range. The wintering ranges of both herd segments and the summer range of the resident segment are included in the Clarks Fork Hunt Unit.

Geographic Scope of Populations and Disease and Change in Land Use

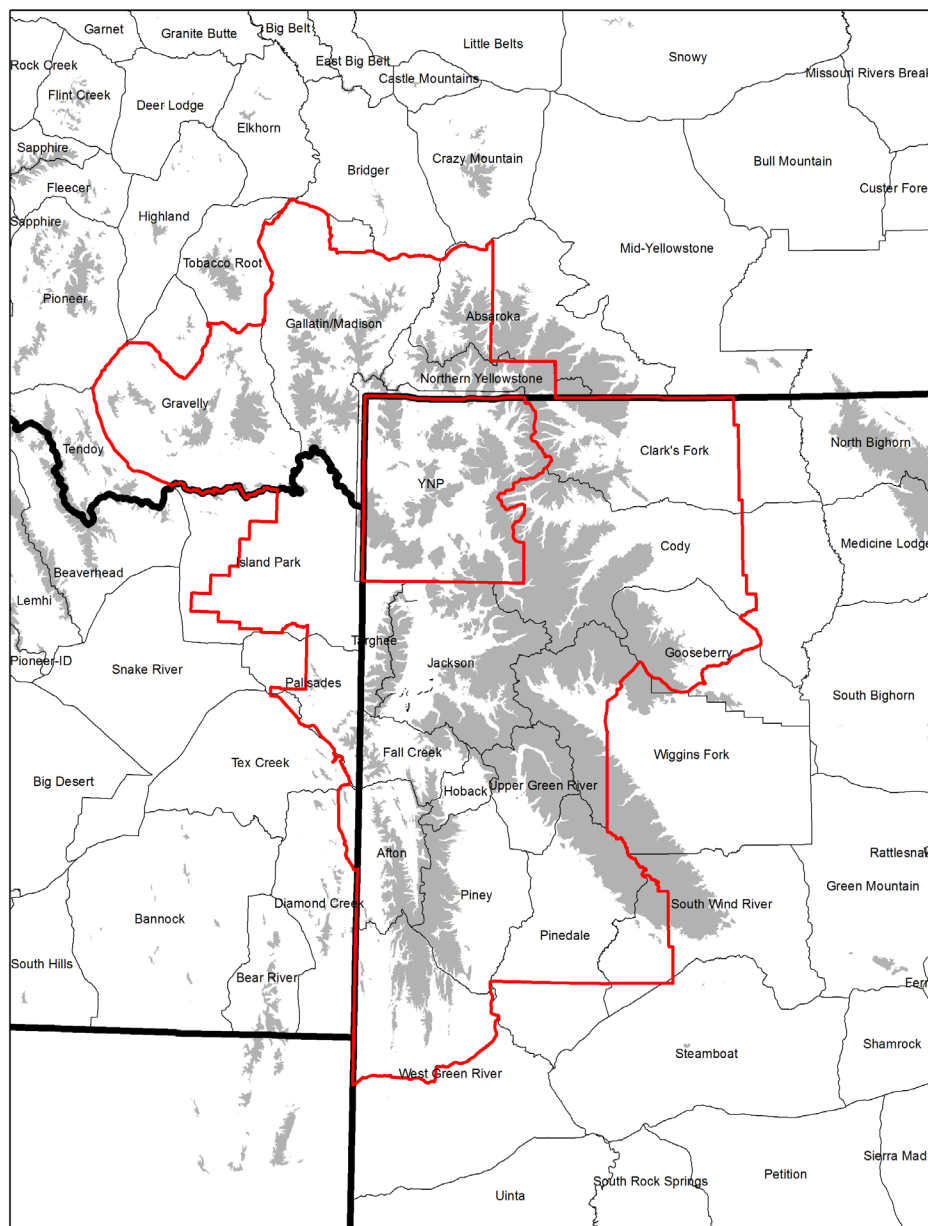


FIGURE 2-4 Elk management units in Montana, elk hunt units in Wyoming, and game management units in Idaho in relation to the designated surveillance area and the YNP boundary, as of 2014 (red lines). Elevations above 2,500 m are shown in gray. SOURCE: MDFWP and WGFD data provided to committee.

The productivity of the migrant herd has declined markedly, with calf recruitment decreasing 70% over 21 years and pregnancy decreasing 19% in 4 years. The decline may be partly due to increased dryness in the region, particularly on summer ranges, with shorter durations of green-up occurring (perhaps 16 days) since 2002. Also, the migrant Clarks Fork elk are exposed to four times as many grizzly bears and wolves as resident elk (Middleton et al., 2013a). Along with the Cody herd and the Jackson herd, the Clarks Fork elk have experienced reduced calf recruitment (4%-16%) and population growth rate (2%-11%) from 1987 to 2010 (Middleton et al., 2013c). During this time, some grizzly bears shifted their diets to less predation on trout and likely more predation on elk calves. This diet shift may have been a result of the decline in cutthroat trout in and around Yellowstone Lake, which in turn is due to the invasion of lake

Revisiting Brucellosis in the Greater Yellowstone Area

trout (Middleton et al., 2013c). There is debate on whether the grizzly bear population has increased inside YNP (Schwartz et al., 2006; Hamlin and Cunningham, 2009); however, the population has increased in areas outside of YNP (Schwartz et al., 2006). The combination of more bears and shifts in bear diets could have acted synergistically to reduce calf recruitment of migratory elk in this herd (Middleton et al., 2013c).

The largest elk groups in this area tend to be in open range land systems. Wolf numbers are positively correlated with larger groups in open areas (Brennan et al., 2015), while in forested areas elk group sizes tend to be smaller in the presence of wolves (Creel and Winnie, 2005). As a result of wolf presence in large open areas in this region, there are a few very large elk groups (see Figure 2-6).

Elk Herds East of YNP

Herds east of YNP (see Figure 2-4) totaled 17,425 elk in 2015, with an objective of 17,065 (see Table 2-2). Numbers in eastern herd units could be markedly higher than numbers counted based on model estimates that correct for sightability (personal communication, B. Scurlock, Wyoming Game & Fish Department [WGFD]).

Herds south and southeast of YNP (see Figure 2-4) totaled 37,410, with an objective of 35,577 (see Table 2-3). Elk population trends in Wyoming herds east, southeast, and south of YNP are shown in Figures 2-7, 2-8, and 2-9.

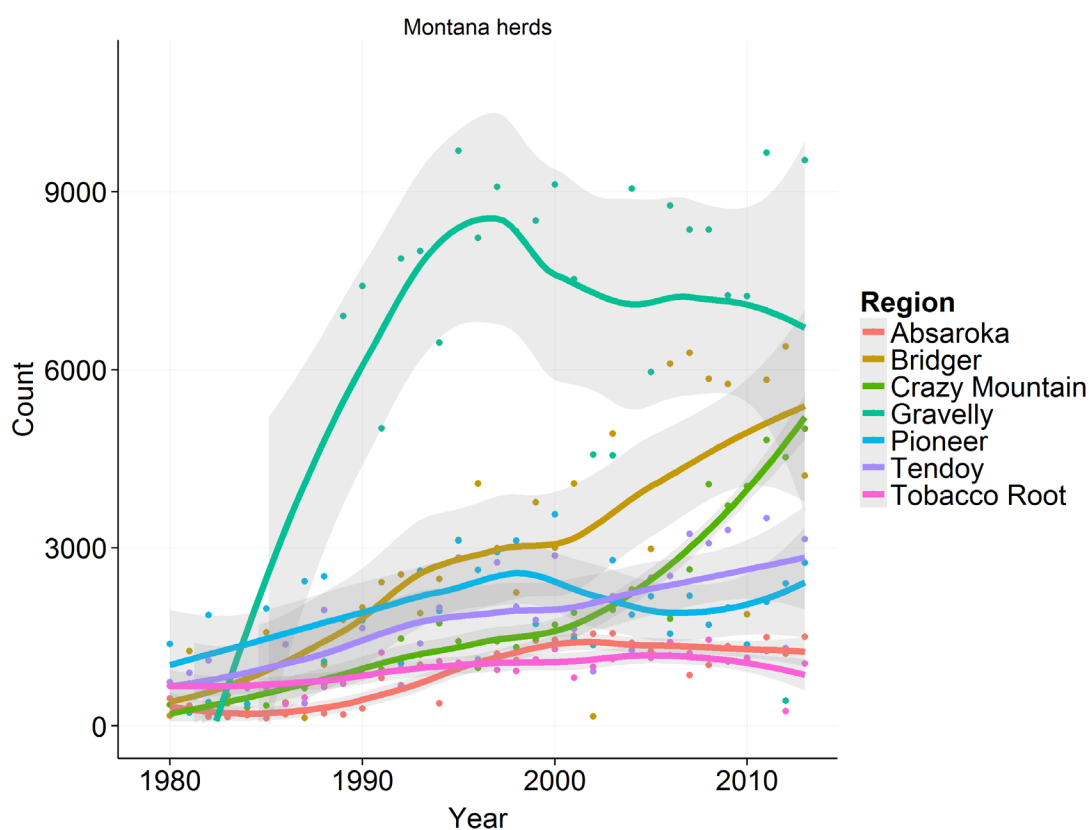


FIGURE 2-5 Trends in elk numbers in Montana EMUs. These EMUs are located just beyond the DSA, except for Gravelly. The gray bands represent the 95% confidence interval on a locally weighted scatterplot smoothing. SOURCE: MDFWP data provided to committee.

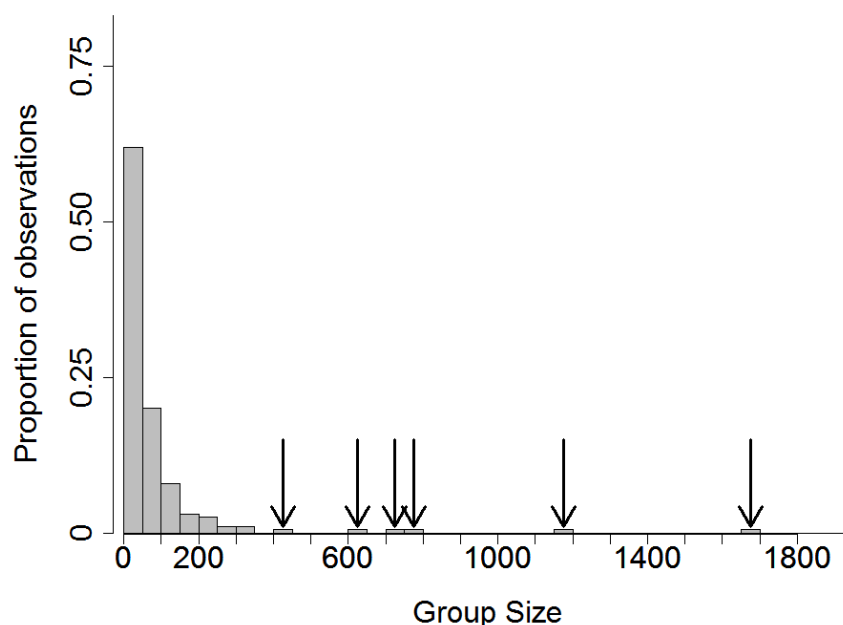
Geographic Scope of Populations and Disease and Change in Land Use

FIGURE 2-6 Histogram of the elk group size distribution from the eastern portion of the GYA in Wyoming. Arrows highlight the few, but very large elk groups. SOURCES: Cross et al., 2013; Brennan et al., 2015.

TABLE 2-2 Numbers of Elk in Herds East of YNP in Wyoming in 2015

Elk Hunt Area	Total Counted	Population Objective	Posthunt Estimate
Clarks Fork	2,390	3,300	4,600
Cody	4,205	4,400	6,000
Gooseberry	2,090	2,015	2,000
Medicine Lodge	2,130	3,000	8,216
North Bighorn	6,610	4,350	6,610
Total	17,425	17,065	27,426

NOTES: “Total Counted” is the total number counted from the ground or air during classifications. “Population Objective” is set by the WGFD and “Posthunt Estimate” is statistically modeled and takes into account sightability and survey effort.

SOURCE: Personal communication, B. Scurlock, WGFD.

Elk in Idaho, Southwest of YNP

There are five elk management zones in eastern Idaho that provide habitats for GYA elk (see Figure 2-4 and Table 2-4). These units contain herds that seasonally migrate over relatively short distances from low elevation winter ranges to higher elevation summer ranges. There is some movement between Idaho and YNP, Grand Teton National Park (GTNP), and the Rockefeller Parkway areas in Wyoming. In certain circumstances, Idaho permits emergency winter feeding of elk to prevent excessive mortality in drainages that would affect herd recovery. There is one elk emergency winter feeding area with four feeding sites near the border with Wyoming (personal communication, D. Cureton, Idaho Department Fish and Game).

*Revisiting Brucellosis in the Greater Yellowstone Area***TABLE 2-3** Numbers of Elk in Herds South and Southeast of YNP in Wyoming in 2015

Elk Hunt Area	Total Counted	Population Objective	Posthunt Estimate
Fall Creek	3,813	4,400	4,500
Afton	1,837	2,200	1,837
Upper Green River	2,713	2,500	2,713
Piney	1,736	2,400	3,100
Jackson	11,051	11,000	11,200
Pinedale	2,081	1,900	2,081
West Green River	4,791	3,100	3,225
Hoback	1,104	1,100	1,104
Wiggins Fork	5,663	5,500	5,817
South Wind River	2,621	2,600	—
Targhee	0	200	200
Total	37,410	36,900	35,777

NOTES: “Total Counted” is the total number counted from the ground or air during classifications. “Population Objective” is set by the WGFD and “Posthunt Estimate” is statistically modeled and takes into account sightability and survey effort.

SOURCE: Personal communication, B. Scurlock, WGFD.

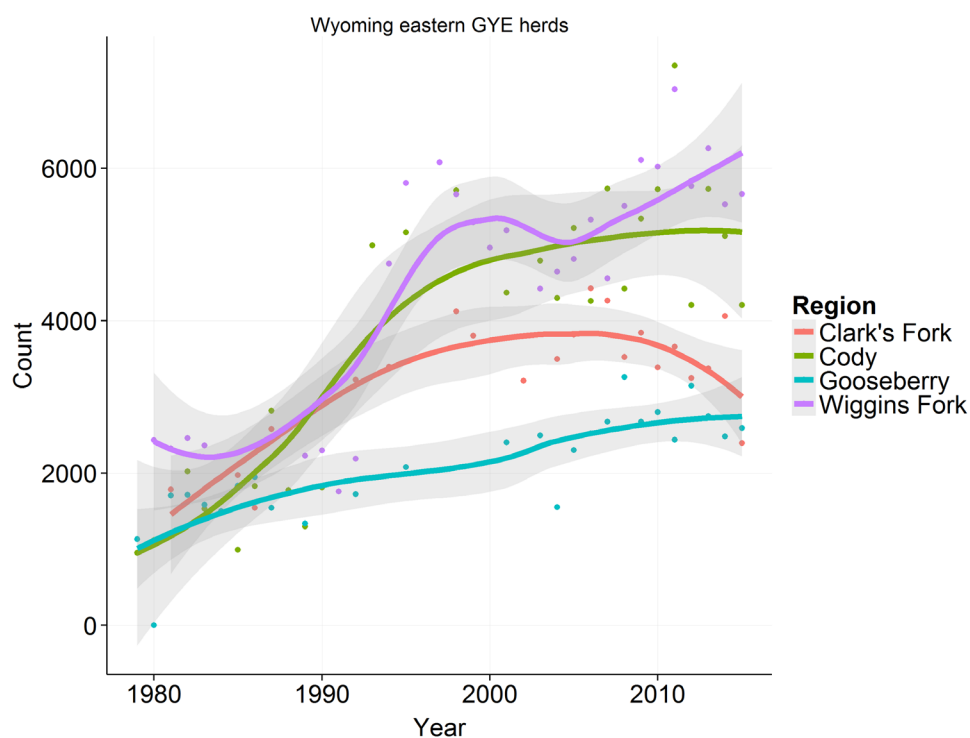


FIGURE 2-7 Elk population trends in herds east of YNP. The gray bands represent the 95% confidence interval on a locally weighted scatterplot smoothing. SOURCE: WGFD data provided to committee.

Geographic Scope of Populations and Disease and Change in Land Use

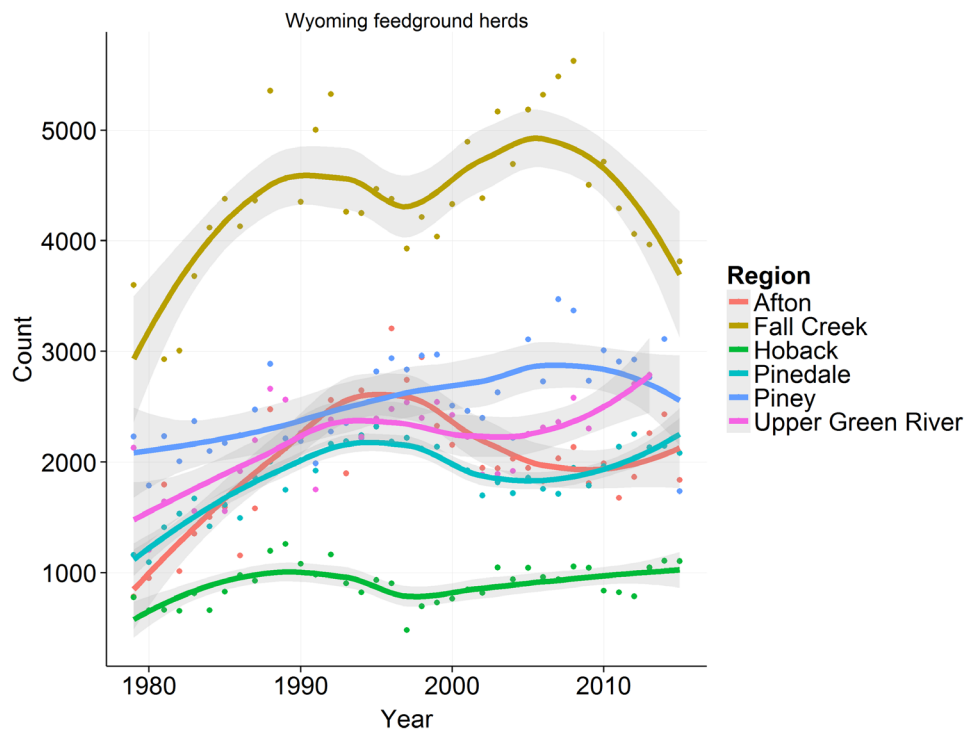


FIGURE 2-8 Elk population trends in herds south and southeast of YNP. This area also has the elk feedgrounds. The gray bands represent the 95% confidence interval on a locally weighted scatterplot smoothing. SOURCE: WGFD data provided to committee.

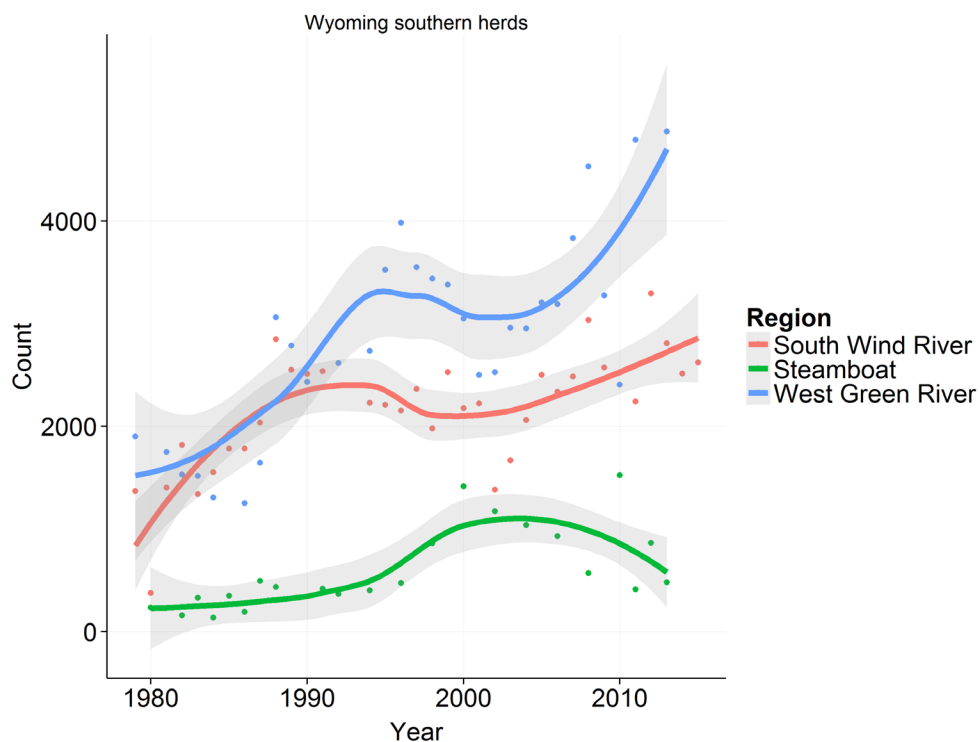


FIGURE 2-9 Elk population trends in herds the furthest south of YNP. The gray bands represent the 95% confidence interval on a locally weighted scatterplot smoothing. SOURCE: WGFD data provided to committee.

*Revisiting Brucellosis in the Greater Yellowstone Area***TABLE 2-4** Elk Herds in Idaho in the GYA

Idaho Elk Management Zone	Count
Island Park	2,512
Teton	220
Palisades	797
Tex Creek	3,885
Diamond Creek	2,352
Total	9,766

NOTE: Idaho elk management zones are listed from north to south.

SOURCE: Cureton and Drew, 2015.

2.6 The Jackson Elk Herds

The Jackson Herd Unit comprises most of the areas south and east of GTNP and the National Elk Refuge (NER), with three elk feedgrounds located in this area (see Figure 2-4). The Jackson elk herds winter on low elevation winter ranges, including the NER, the Gros Ventre drainage, and areas near Moran in GTNP. Many of these elk move to higher elevation summer ranges across a broad area to the north, including southern YNP (Boyce, 1989; Smith and Anderson, 2001; Cole et al., 2015).

The management objective determined for this area is 11,000 elk, which is based on judgment, past experience, and balance of conflicting objectives of different stakeholders. On average, there were 11,690 elk counted from 2009-2013 and 11,051 were counted in 2015 (WGFD, 2014; see Table 2-4). As many as 19,000 elk were estimated in the mid-1990s, but annual harvests have reduced the population (USFWS and NPS, 2007). Herd management goals were to feed 5,000 elk on the NER, 3,500 elk in the upper Gros Ventre feedgrounds and native winter ranges east of Crystal Creek, and 2,500 elk on other native winter ranges (WGFD, 2014). The number of elk on native winter ranges has decreased dramatically over the past decade (USFWS and NPS, 2007). On average, 1,307 elk were harvested by 3,082 hunters per year from 2009-2013. The NPS and the Wyoming Game and Fish Commission also carry out elk reductions based on yearly recommendations in two areas just outside the east boundary of GTNP.

An average of 536 Jackson herd elk have wintered in GTNP from 1989-2003. The objective is to support an average of about 356 elk in GTNP, with numbers ranging between 137 and 857 (USFWS and NPS, 2007). The NPS philosophy for national parks is to contribute to the conservation of species at larger landscape scales. However, there are no allowances for permitting elk or bison populations to exceed natural densities within GTNP, even when this would contribute to natural population levels for the larger landscape (USFWS and NPS, 2007).

An elk reduction program in GTNP was authorized by Congress in 1950. Removals occur in the Fall in two hunt areas east of the Snake River but within the boundaries of GTNP and are coordinated between the NPS and WGFD (personal communication, Sue Consolo-Murphy, National Park Service, February 23, 2016). In the mid-1990s, densities of elk were 2.5-fold higher in GTNP than densities outside of GTNP, likely as a result of the relative lack of hunting inside GTNP compared to outside of GTNP (Smith and Anderson, 1996). Smith and Anderson (1996) also concluded that elk numbers inside GTNP were not being regulated through food limitation and density dependence because they spend winter and are fed on the NER, and thus they argued that hunting removals are warranted.

In 2014, there were 129 wolves in 17 packs in the Jackson herd area (packs south and southwest of YNP excluding Wind River Reservation and Prospect packs) (Jimenez and Becker, 2015). As of the winter of 2004, the total number of elk killed by wolves each winter in the Gros Ventre portion of the Jackson herd area was estimated to represent less than 1% of the herd (USFWS and NPS, 2007; WGFC, 2007). Wolves incidentally preyed on the NER until 2004/2005; 18 elk were killed in 2004/2005 and 63 were killed in

Geographic Scope of Populations and Disease and Change in Land Use

2005/2006 (USFWS and NPS, 2007). Grizzly bear numbers were positively correlated with calf:cow ratios in this area, more so in unfed than in fed elk (Foley et al., 2015).

2.7 Elk Feedgrounds

Currently, 22 elk feedgrounds are maintained in Wyoming by the WGFD, independently of the NER. Feedgrounds are mostly located adjacent to active cattle allotments within the Bridger-Teton National Forest (BTNF) and along boundaries between U.S. Forest Service (USFS) lands and private lands. Bienen and Tabor note two reasons for feeding, including “keeping brucellosis infected elk from foraging on cattle ranches, and maintaining consistently higher numbers of elk than the available range could support, which satisfies hunters and outfitters and brings revenue to the state” (Bienen and Tabor, 2006). WGFD states three reasons for maintaining the feedgrounds: (1) to prevent depredation on stored crops, (2) to prevent elk-livestock comingling, and (3) to reduce winter elk mortality (WGFD, 2011). However, there is some disagreement about the benefits of feedgrounds (Bienen and Tabor, 2006). In the absence of feeding, elk disperse and give birth alone, which limits disease transmission. Additionally, there is concern that the mortality from an epidemic of chronic wasting disease that could be facilitated by high elk densities on feedgrounds would exceed any losses resulting from reducing or eliminating feeding.

From 1982-1987, the number of elk counted on the feedgrounds, including the NER, increased from 17,770 to 20,145, but since then the number has been relatively stable in the range of 20,000 to 26,000 (Cross et al., 2010a). From 1998-2013, the NER has fed 5,000-8,000 elk (USFWS and NPS, 2007), which means that approximately 15,000-18,000 elk have been fed on the other feedgrounds since 1998. Since 1998, WGFD tried to reduce large elk aggregations on several feedgrounds by distributing food across a broader area and by stopping feeding earlier in the year (Cross et al., 2013). Targeted elk hunts have been implemented in some areas of southwestern Montana and western Wyoming to disperse large groups, move them away from cattle, and reduce population sizes.

In theory, supplemental feeding would reduce negative effects of dry growing seasons and severe winters on forage availability, which would then result in increased elk reproduction and survival (Foley et al., 2015). However, one study found no evidence that feedgrounds affected midwinter calf:cow ratios (Foley et al., 2015). Calf:cow ratios of fed elk were more strongly correlated with environmental factors (snow and summer rainfall), while calf ratios of unfed elk were more strongly correlated with predator densities, particularly bear density. In contrast, an earlier study found that survival of calves supplementally fed in winter exceeded survival of calves not fed (Smith and Anderson, 1998).

Population growth is also affected by juvenile and adult survival (Lubow and Smith, 2004). However, variation in juvenile survival is primarily affected by environmental conditions—particularly snowpack and duration of winter—and is little affected by feeding (Smith and Anderson, 1998). Also, female elk that fed on feedgrounds had negligibly higher survival rates than unfed elk, and any differences in survival due to feeding were due to effects on older animals, which have lower reproductive values (Foley et al., 2015).

Supplemental feeding can alter the seasonal migrations of elk (Jones et al., 2014). Fed elk migrate shorter distances, arrive on summer ranges later, and depart from summer ranges earlier than unfed elk. Feeding disrupts the migration of fed elk from the timing of spring green-up, and it decreases the time elk spend on summer range by 26 days, thereby reducing access to quality forage (Jones et al., 2014). If supplemental feeding were phased out, elk might make greater use of summer ranges to at least partially compensate for the loss of feed. Supplemental feeding of elk also increases dense aggregations which in turn increases stress levels; this has been detected through increases in glucocorticoid, a metabolite associated with stress that has been hypothesized to reduce immune function and increase disease susceptibility (Forristal et al., 2012). Relocating, reducing, or eliminating feedgrounds are options that have previously been considered but not pursued by WGFD in its Brucellosis Area Management Plans (WGFD, 2011). Reasons cited by WGFD for not pursuing these options include land availability constraints with relocating feedgrounds (including permitted grazing allotments) and lack of support from various constituencies (agriculture, land management agencies, sportsmen) for reducing or eliminating feedgrounds. However, as part of

Revisiting Brucellosis in the Greater Yellowstone Area

a Target Feedground Project, major reductions in the length of the feeding season have already occurred at certain feedgrounds since 2008, and minor reductions have occurred at other feedgrounds since 2009.

2.8 The National Elk Refuge

In 1912, the NER was created as a place for supplemental elk feeding that would mitigate the loss of natural winter range and minimize impacts to livestock operations. Historically, elk moved longer distances to areas, including the upper Gros Ventre Basin, Idaho, the Green River area, and in severe winters, the Red Desert (Murie, 1951; Cole, 1969; Boyce, 1989; Cromley, 2000; USFWS and NPS, 2007). Recently, human settlement and conversion of winter range to livestock grazing areas has shortened migration routes and caused elk to remain in Jackson Hole (USFWS and NPS, 2007). Supplemental feeding increases the nutritional status¹ of 68% to 91% of the Jackson elk herd and reduces winter weight loss, particularly in severe winters (Wisdom and Cook, 2000; USFWS and NPS, 2007).

The number of elk fed on the NER has varied from about 5,000-11,000 between 1971-1997, and from 5,000-8,000 between 1998-2013. The Bison and Elk Management Plan calls for a reduction to 5,000 elk on the NER (USFWS and NPS, 2007). The population objective of 5,000 elk for the NER is distinct from the population objective of 11,000 for the entire Jackson herd unit set by WGFD. The herd objective for the NER is set at a level that is in line with U.S. Fish & Wildlife Service (USFWS) policy for refuges to contribute to natural population densities and natural levels of variation at larger landscape scales, especially when habitat has been lost in the surrounding landscape or ecosystem (USFWS and NPS, 2007).

Given concerns over the negative impacts of supplemental feeding on brucellosis transmission, it is pertinent to determine how many elk could be supported on native ranges if feedgrounds were to be phased out. In modeling the number of elk that could be supported across an area corresponding to the Jackson herd unit, Hobbs and colleagues (2003) used a “Forage Accounting Model” to estimate forage production, snow cover, and resulting forage availability for different habitat types. The model indicated that supplemental feeding is necessary to support current numbers of elk in winters with above average snowpack, but supplemental feeding far overcompensates for the loss of winter range in winters that have average or below average snowpack (Hobbs et al., 2003). Without supplemental feeding, about half as many elk could be supported compared to current numbers in winters with average snowpack. However, reductions in forage availability in severe winters are natural occurrences. The model indicated that habitat removals due to human settlements and livestock grazing have had negligible effects on forage availability (Hobbs et al., 2003).

According to the 2007 elk and bison management plan, a long-term goal is to implement a variety of actions to transition from intensive supplemental winter feeding on the NER to a greater reliance on free-standing forage (USFWS and NPS, 2007). This would need to be carried out with objective criteria and adaptive management actions that would be developed in collaboration with WGFD.

3. CHANGES IN LAND USE AND CONSEQUENCES FOR ELK

Changes in land ownership in areas outside of YNP have affected elk distributions and the ability of state wildlife authorities to manage elk populations. In three elk hunting districts (HDs) just north of YNP, there has been a shift in property ownership to more owners who are interested in natural amenities and who exclude hunters in order to support elk for their own enjoyment, which consequently has created refugia for elk (Haggerty and Travis, 2006). In those three HDs numbers—313, 314, and 317—18% of the winter range is privately owned in one district (HD 313) while 71% and 46% of winter range is privately owned in the other two districts (HD 314 and 317), respectively (Haggerty and Travis, 2006). MDFWP has been able to utilize a combination of general and late-season hunts to achieve population targets in HD 313,

¹Nutritional status indicates the degree to which an animal’s nutritional requirements are being met through forage intake. Nutritional status will decrease when requirements are not being met, and it will increase when intake exceeds requirements.

Geographic Scope of Populations and Disease and Change in Land Use

but this has proven to be more difficult in HDs 314 and 317, because the lands are “out of administrative control” (Haggerty and Travis, 2006). Similar and even more pervasive land ownership changes have taken place in the Paradise Valley (north of the Northern Yellowstone Management Unit) and in the Madison River Valley (west of YNP). These land use and land ownership conversions could have contributed to a much larger fraction of the northern elk herd now being found outside of YNP in the winter and in larger and denser groups than previously found.

More people are also settling across the GYA. From 1990-2010, the population of census blocks in and near the GYA increased nearly 50%, with much of that growth occurring in rural home development (McIntyre and Ellis, 2011). From 1970-1999, the population in the GYA increased by 58%, with rural areas increasing by 350% due to exurban housing densities, demonstrating that developed land in the GYA is increasing faster than the rate of population growth (Gude et al., 2006). The GYA consists of the 145,635 km² of land, with 32% privately owned, 32% managed by the USFS, 19% by the Bureau of Land Management (BLM), and 7% managed by the NPS (Gude et al., 2007). Using the current rates of population growth to predict future land use scenarios and their potential impact on biodiversity, Gude and colleagues (2007) predicted that 10% of elk winter range and 24% of wildlife migration corridors would be affected in 2020.

With many core winter ranges north and northwest of YNP in private ownership, MDFWP has identified a number of management challenges. These challenges arise from a large fraction of the elk population not being available to hunters due to reduced access to public land and adjacent private land; increases in landowners who have less interest in allowing elk hunting; and elk that have shifted onto privately owned lands during the hunting season (Proffitt et al., 2010b). However, as of the writing of this report, a proposed option in the Montana Fish & Wildlife Commission’s Brucellosis 2017 Annual Work Plan would allow for landowners in the Red Lodge area, which is outside the DSA, to request that a very limited number of potentially infected elk (no more than 10) be culled to prevent contact with livestock (French, 2016).

Changes in land use can also potentially increase the risk of elk-cattle contact. Across the GYA, scrub/shrub and grasslands are the predominant land cover types on private lands (35% and 26%, respectively), and they are the types most likely to be used for livestock grazing (McIntyre and Ellis, 2011). Winter ranges for large mammals (elk, mule deer, pronghorn antelope) also occur primarily on scrub/shrub (9,804 km²) and grassland/herbaceous (7,001 km²) land cover types. Consequently, increased development of private lands on land cover types that are used by both livestock and large mammalian wildlife (including elk) could result in an increasing number of wildlife finding refugia from hunting on exurban land holdings (Haggerty and Travis, 2006; Gude et al., 2007; McIntyre and Ellis, 2011). Increased elk-livestock interaction could occur in some areas where elk prefer private lands with livestock over lands where public hunting occurs (Proffitt et al., 2010b). Although exurban development could reduce elk-livestock interactions by reducing livestock numbers, this could be offset by increased elk-elk transmission due to denser concentrations of elk on exurban refugia.

4. BISON POPULATIONS AND DISTRIBUTIONS

4.1 The Yellowstone Bison Herds

The Yellowstone bison population consists of two herds: a central herd and a northern herd, with some intermixing between them (Gates et al., 2005; Olexa and Gogan, 2007). The range for the central herd includes the Hayden and Pelican Valleys in the east, across to the Firehole Valley and the Madison River Valley in the west (see Figure 2-10). The range for the northern herd is at lower elevations and includes the Lamar River Valley in the east and the Gardiner Basin in the west. Under the Interagency Bison Management Plan (IBMP), bison are allowed to use habitats outside the northern and western boundaries of YNP (Zone 2 and Eagle Creek, see Figure 2-10).

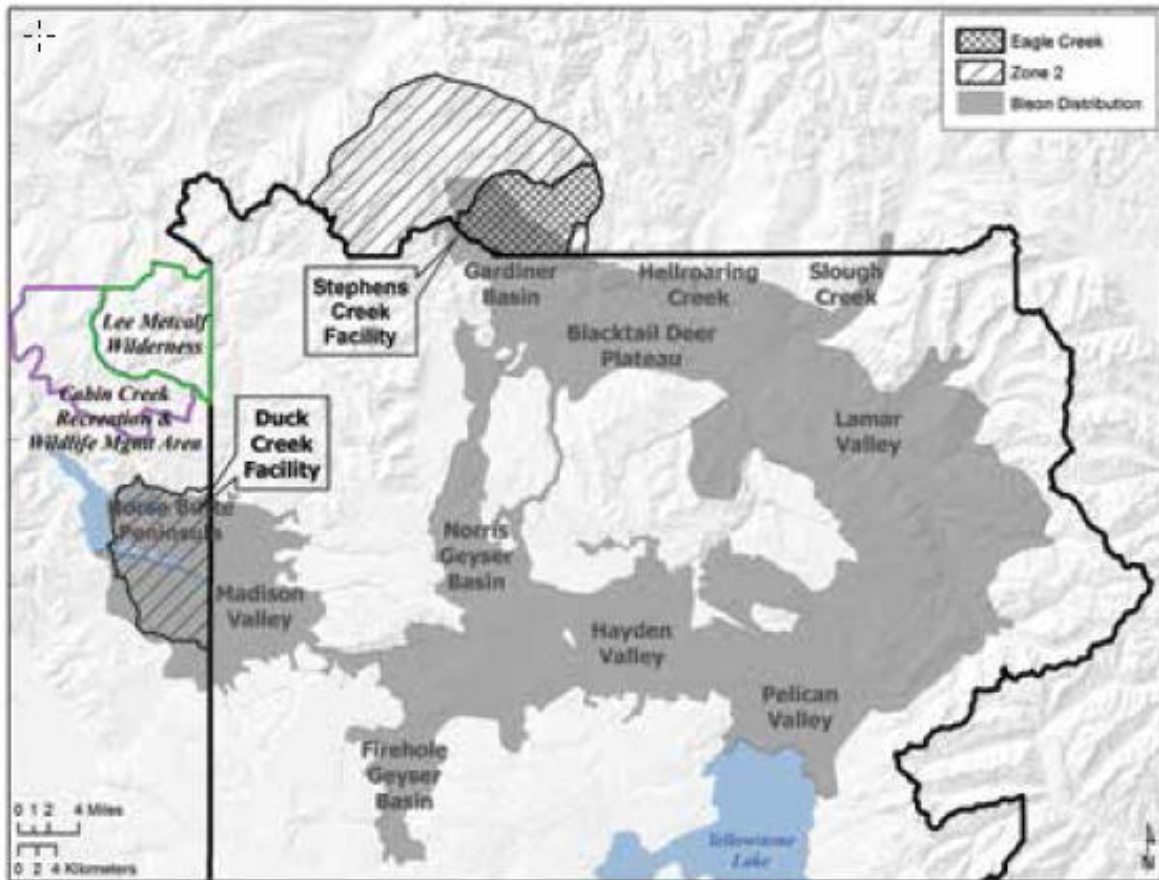
Revisiting Brucellosis in the Greater Yellowstone Area

FIGURE 2-10 Bison range distribution conservation areas and Zone 2 bison tolerance areas. SOURCE: Wallen et al., 2015.

In 1966, the total bison population was 366 and had been managed through periodic herd reductions. In 1968, a natural regulation policy was adopted for bison and elk, with the hypothesis being that populations would naturally achieve a dynamic equilibrium with forage production without human intervention. The bison population grew steadily from 1968-1995 (see Figure 2-11). The first removals outside YNP boundaries occurred in 1992, with considerable numbers of bison removed in winters of 1994-1998. In 2006, the population grew in size to 5,015 animals. Bison hunting was first allowed outside the YNP boundaries in 2005-2006, and a substantial number of bison were hunted in the following years. Due primarily to management removals from 2005-2008, the total population was reduced to less than 3,000 in 2009. Since that time, the total bison population has increased to nearly 5,000 in 2014, which increases the population average to about 4,000 over the longer term. Notably, most of this increase occurred in the northern herd, which has more than doubled in size since 2008; meanwhile, the central herd has remained nearly constant in size. In 2015, YNP managers recommended removing or hunting approximately 900 bison per year in the two following winters to achieve a population target of 3,500, as recommended in the IBMP (Geremia et al., 2014a). The number of bison that can actually be removed depends on the number that cross the YNP boundary; however, it is realistic to assume sufficient numbers would emigrate given the current size of the population.

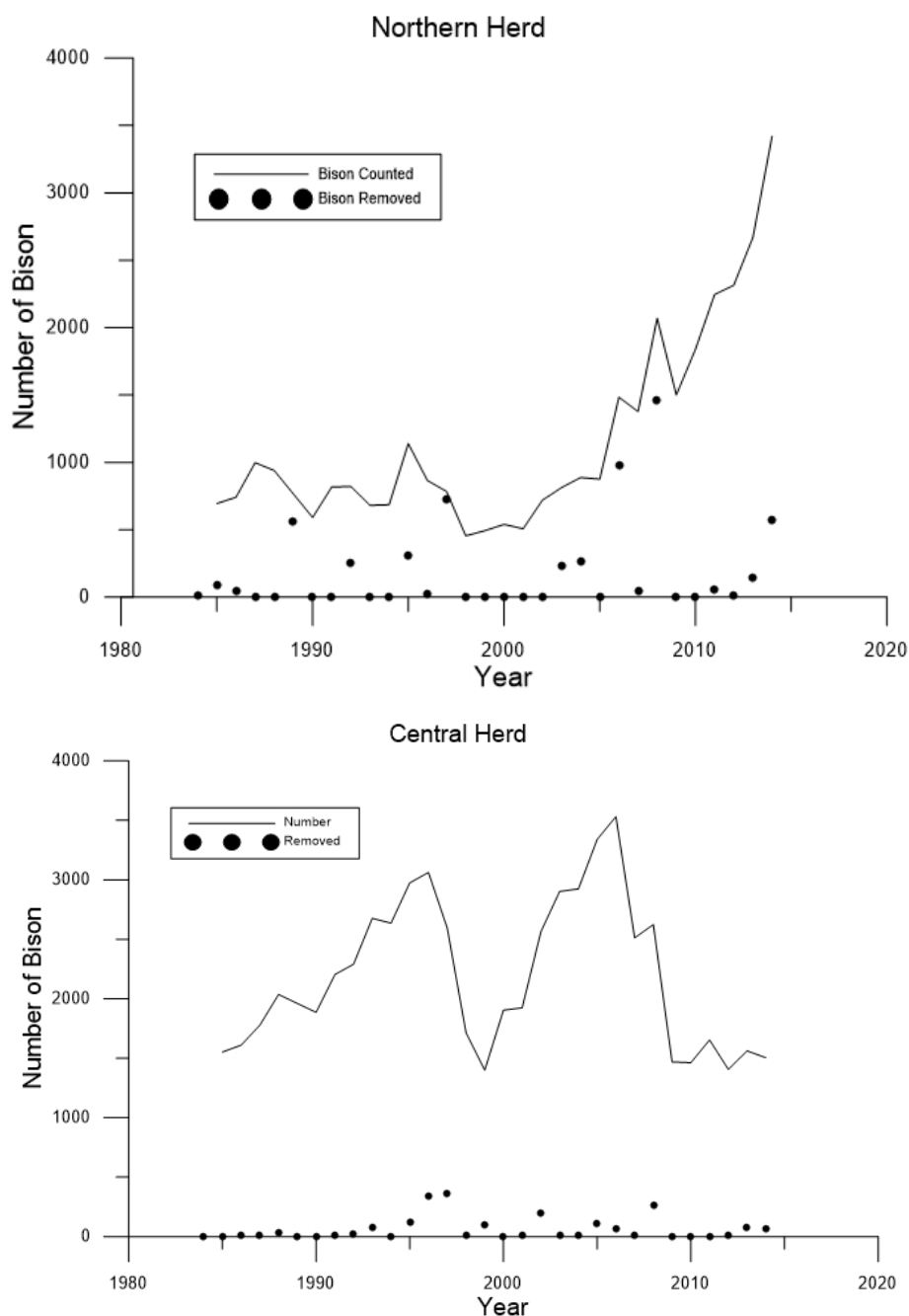
Geographic Scope of Populations and Disease and Change in Land Use

FIGURE 2-11 Bison counts and annual removals, northern and central herds. SOURCE: Geremia et al., 2014b.

Bison migrate seasonally along elevational gradients: moving from higher-elevation summer ranges to lower elevations during autumn through winter, and returning to summer ranges in June (Meagher, 1989; Bjornlie and Garrott, 2001; Bruggeman et al., 2009; Plumb et al., 2009). Migration to lower elevations is primarily driven by earlier snow fall and greater snow depths at higher elevations in autumn and early winter. As the bison population increased, more bison began migrating earlier to lower elevation winter ranges for better access to food resources (Meagher, 1989; Bruggeman et al., 2009; Plumb et al., 2009). In the spring, bison progressively migrate to higher elevations, following the progressive snow melt and green-up with increasing elevation.

Revisiting Brucellosis in the Greater Yellowstone Area

Bison movements out of YNP are driven by a combination of density and snow conditions that reduce forage availability. Density dependent dispersal has been observed in many animal populations (Owen-Smith, 1983; Pulliam, 1988). Since 1998, more than 6,000 bison have been removed from the two dispersal areas outside the northern and western boundaries during their annual winter migrations to lower elevations, and the total population has been kept in the 3,000-5,000 range since 2002. However, the northern range has now become a dispersal area for the central herd; numbers in the northern herd have more than doubled; and animals crossing the northern boundary are coming from the central herd.

An analysis of bison removals versus population size showed that there were generally few removals when the population was below 3,000. Above the threshold of 3,000, bison removals markedly increased and removals were highly correlated with population size when snow water equivalent was above 17 inches. It was also suggested that exceptionally large numbers of bison would leave YNP when the snow pack melts and refreezes to create an ice layer, as occurred in the winter of 1996-1997. A more recent analysis using data through 2008 indicated that in average winters, most movements outside YNP would be minimal if population sizes are kept <3,500 in the central herd and <1,200 in the northern herd (Geremia et al., 2009). Migration beyond the northern boundary is affected by herd size, snow water equivalent, and forage biomass whereas migration beyond the western boundary is less influenced by these variables (Geremia et al., 2011). Kilpatrick and colleagues (2009) predicted that with 7,000 bison and average snowfall, more than 1,000 bison would leave YNP in 74% of the winters; with 3,000 bison and average snow, more than 1,000 bison would emigrate in 9% of the winters; and with severe snow, more than 1,000 bison would leave in 25% of the winters (see Figure 2-12).

In the past three decades, the increases in bison populations and bison movements outside YNP have been partly attributed to more favorable conditions for bison movement and resultant range expansions. Although road grooming for snowmobiles and coaches could increase population growth and facilitate movements and range expansion (Meagher, 1993), more recent analyses have concluded that road grooming has not affected range expansion or population growth (Gates et al., 2005; Bruggeman et al., 2007). Bison have increasingly used road corridors to travel through certain landscape bottlenecks, such as canyons that connect the central and the northern herd ranges (Gates et al., 2005; Bruggeman et al., 2006, 2007, 2009). The resultant increased connectivity between the central and northern herds has likely contributed to increased numbers of animals exiting the northern boundary.

Bison population growth rate decreases at higher population densities (Fuller et al., 2007). This is because bison become increasingly resource limited at higher population densities, despite the added resources resulting from range expansion as was seen in the 1980s and 1990s. Despite the declining population growth rate at higher densities and removals at the boundaries, population growth rates have remained positive, even at high densities (see Figure 2-12).

The use of an ecosystem model to estimate food limited carrying capacity can be useful for predicting population dynamics (Coughenour, 2005; Plumb et al., 2009). Coughenour (2005) predicted that a mean bison population size of 6,000 could be sustained at food limited carrying capacity with no removals at the boundaries. This is in comparison to the actual population of 5,000 where more bison could theoretically be supported by the forage base. However, bison are intolerant of increased levels of competition and nutritional stress at higher densities and prefer to migrate beyond the designated dispersal areas to maintain adequate nutritional status. Also, elk compete with bison for forage due to overlapping diets and habitat, and bison numbers are affected by elk abundance (Coughenour, 2005). The decrease in elk on the northern elk winter range could therefore have contributed to increased numbers of bison.

4.2 The Jackson Bison Herd

The Jackson bison herd is jointly managed by the NER, GTNP, WGFD, and BTNF. Bison were first introduced into GTNP near Moran in 1964 and were allowed to free range in 1969, enabling bison to establish well-defined seasonal movement patterns in GTNP. However, since the winter of 1975-1976, most of the herd has wintered on the NER. In 1980, bison discovered the NER feedlines and subsequently the herd greatly increased in size. Bison were initially culled or hunted, but no reductions have taken place

Geographic Scope of Populations and Disease and Change in Land Use

since 1990. WGFD reinitiated hunting in 1998 outside the NER and GTNP; however, few have been killed because most habitats are inside the NER or GTNP. In 1990, the Jackson bison population was approximately 110; in 1998, it increased to about 430; and in 2006, it had increased further to about 950 (USFWS and NPS, 2007). The Bison and Elk Management Plan (USFWS and NPS, 2007) calls for a reduction to 500 bison and 5,000 elk. During feeding operations for elk on the NER, bison are fed in order to minimize disruptions with elk feeding operations. After feeding is discontinued in late winter or early spring, the bison herd moves north of the NER to spring ranges, then moves further north to summer ranges on the east side of GTNP. Calving occurs on both the spring and summer ranges.

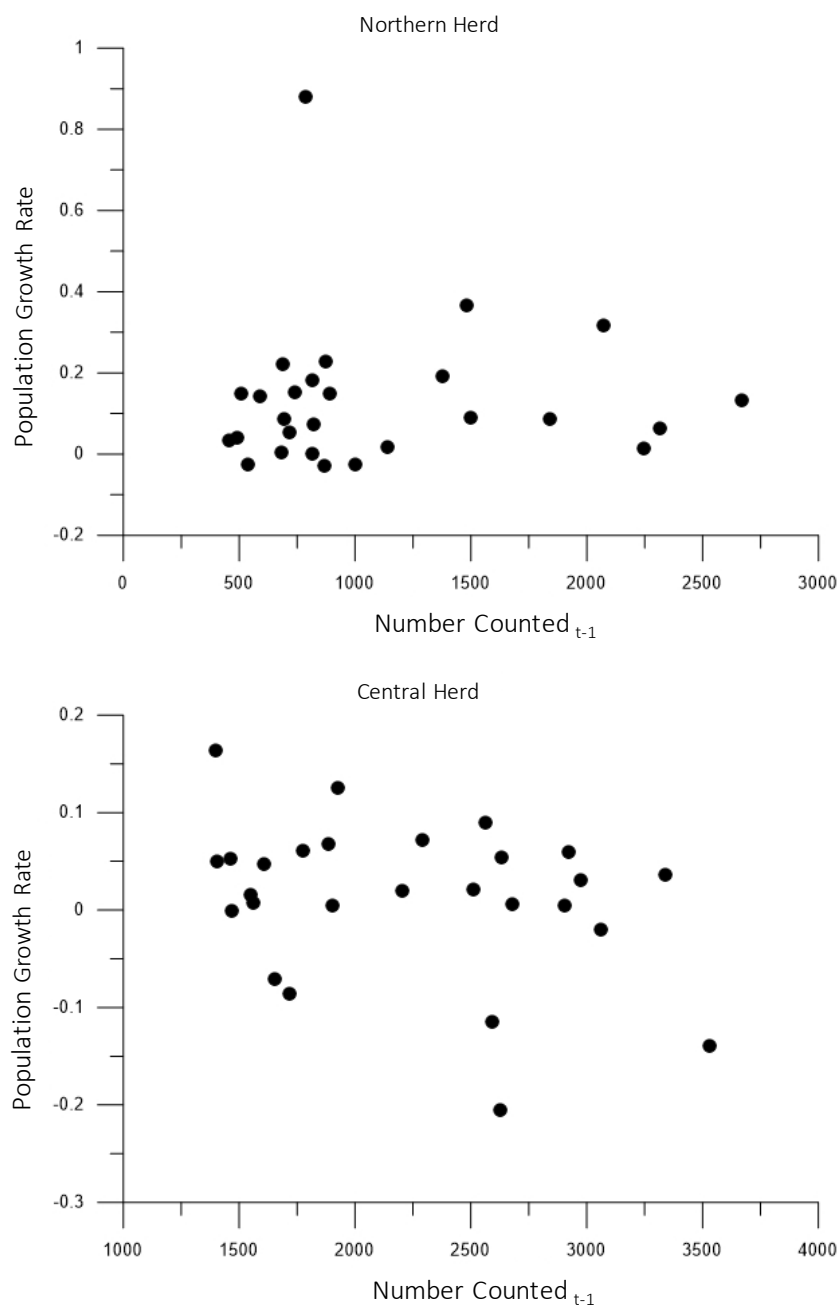


FIGURE 2-12 Bison population growth rates versus population sizes in the previous year, northern and central herds. SOURCE: Geremia et al., 2014b.

*Revisiting Brucellosis in the Greater Yellowstone Area***5. LIVESTOCK**

There are approximately 450,000 cattle and calves in the GYA comprising those in Bonneville, Caribou, Franklin, Fremont, and Teton Counties in Idaho; Gallatin, Madison, and Park Counties in Montana; and Lincoln, Park, Sublette, and Teton Counties in Wyoming (NASS, 2011; Schumaker et al., 2012). Approximately 85% of the operations are cow-calf producers with open-range grazing in summer and pasture supplemented with hay during the winter. Within the DSAs, there are 296 herds in Montana, 242 in Wyoming, and 191 in Idaho (USDA-APHIS, 2014).

Since 1998, cattle operations immediately adjacent to YNP have been reduced as part of the IBMP. Private lands just north of YNP have been acquired by USFS for inclusion into the northern bison management area. In 2006, there were 266 cattle in four herds in winter and 677 in nine herds in spring in the northern bison management area (Kilpatrick et al., 2009). More recently, in the northern bison management area, there were just two small (25 each) cattle operations (USDA-APHIS, 2014). In the IBMP western bison management area, there were no cattle in winter and 686 cattle in nine herds in spring (Kilpatrick et al., 2009). Recently, it was reported that there were four seasonal operators (no year-around operations), with approximately 600 cow-calf pairs utilizing the western management area during summer after June 15 (USDA-APHIS, 2014). Due to the reduced numbers of cattle and management operations that maintain temporal and spatial separation from bison, few cattle have any exposure to infected YNP bison (USDA-APHIS, 2014).

Originally, GTNP had 29 permittees grazing approximately 4,320 animals on 67,640 acres inside GTNP. The number of permittees has decreased to two as a result of permits expiring and ranches ceasing to operate (USFWS and NPS, 2007). The two remaining permittees graze on three grazing allotments that are inholdings: one with 525 cattle animal unit months (AUMs) permitted (264 cattle present) and the others with only horses. Just outside the GTNP are three ranches, with 5,514 cow-calf AUMs on two ranches that seasonally move animals from one area to another and one ranch with 60 breeding stock permitted (55 cattle present) (personal communication, S. Consolo-Murphy, NPS, 2015).

In the three counties in Wyoming at the southern end and just beyond the GYA (Lincoln, Sublett, and Sweetwater Counties), there are approximately 105,000 cattle and 500 producers (personal communication, B. Schumaker, University of Wyoming, 2015). These counties contain portions of 17 WGFD elk herd units and 15 of the 22 feedgrounds not including the NER. In conducting a cost-benefit analysis of various brucellosis management options, a risk map was produced of elk-cattle interactions for this tri-county area (Kauffman et al., 2013), which is a somewhat preliminary approach, but one that has considerable potential for use in the future.

While there are many legally designated grazing allotments throughout the GYA (see Figure 2-13), many of them are not active. The committee was unable to locate maps of all active versus non-active allotments throughout the GYA. However, the BTNF provided the committee with information showing permitted livestock numbers, turn-on and turn-off dates, head-months, and AUMs for each allotment (personal communication, T. O'Conner, USFS, 2016). In the BTNF, there are 63 active grazing allotments with approximately 99,000 permitted cattle (see Figure 2-14). A total of 34,337 livestock, 110,892 head-months, and 135,603 AUMs are permitted. The permits included mature cows with a nursing calf, yearlings, and bulls. Turn-on dates varied from June 1 to July 15 and turn-off dates generally varied from September 15 to October 15. In Idaho, there are currently 163 resident cattle herds within the DSA with approximately 15,000 head; there are also 80 seasonal herds that use USFS, BLM, and private lands with approximately 16,000 head (personal communication, B. Barton and D. Lawrence, Idaho Department of Agriculture, 2015).

Although livestock numbers have been reduced or closely managed immediately adjacent to the national parks, there are large areas of private lands and grazing allotments that have considerable overlap with elk throughout the GYA.

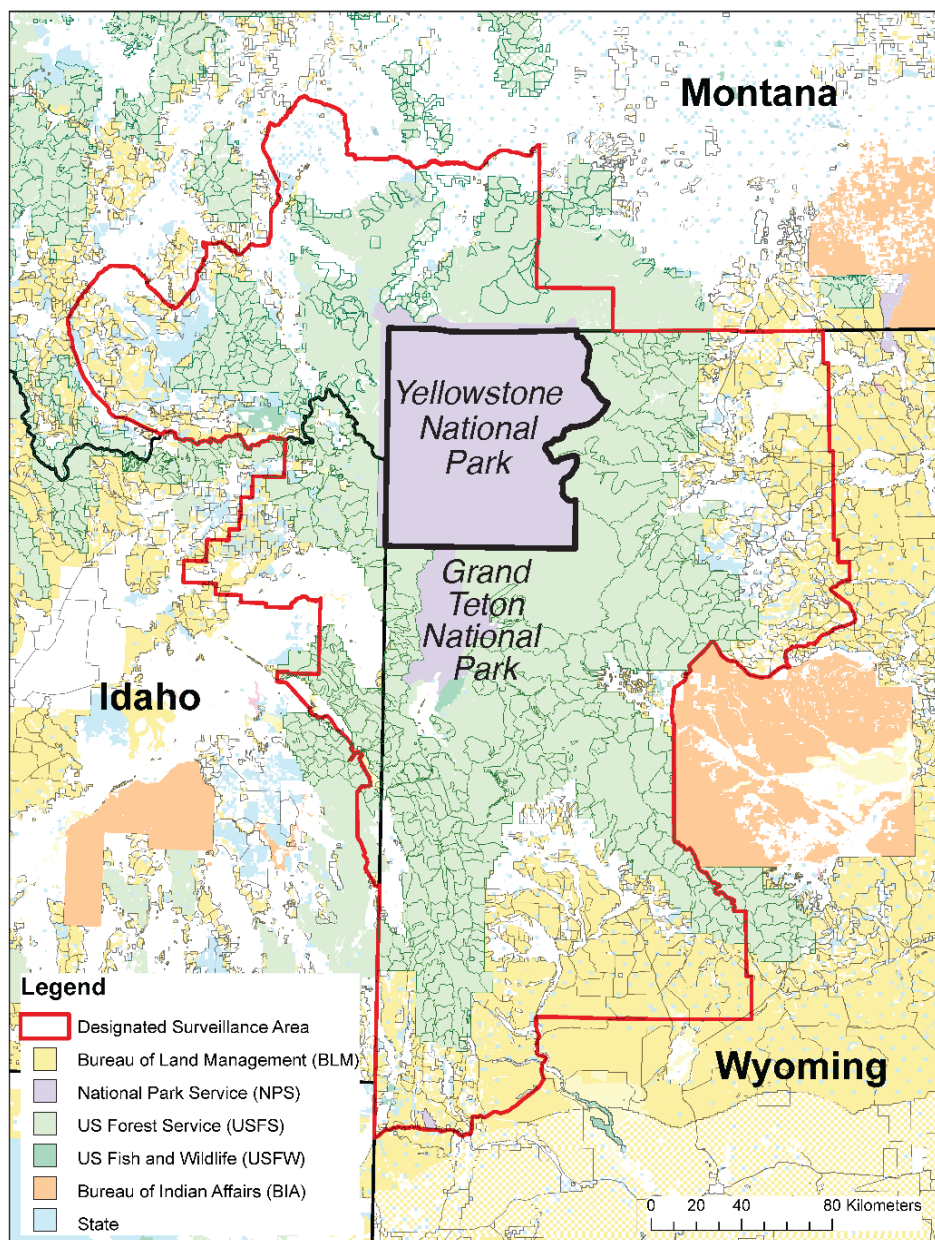
Geographic Scope of Populations and Disease and Change in Land Use

FIGURE 2-13 Grazing allotments throughout the GYA. Each of the drawn polygons is an allotment and the current use of many allotments across the entire region were not easily accessible. SOURCES: BLM (2014) and USFS (2008, 2009, 2015).

6. IMPLICATIONS OF CHANGING CLIMATE FOR ELK AND BISON

Climate change in the GYA has implications for elk and bison numbers and distributions and, thus, brucellosis in the GYA. A recent analysis of historic climate data concluded that over the past 100 years minimum temperatures have increased 2.9°F and maximum temperatures have increased 1.2°F (Northern Rockies Adaptation Partnership, 2014). Using climate model outputs from the Coupled Model Intercomparison Project, maximum temperature in the GYA is expected to rise 5-10°F and minimum temperature is projected to rise 7-12°F. Winter maximum temperature is predicted to rise above 32°F in mid-century,

Revisiting Brucellosis in the Greater Yellowstone Area

and summer temperatures predicted to rise by nearly 5°F by mid-century and nearly 10°F by the end of the century (Littell et al., 2011). Predictions for precipitation are uncertain, but there could be a slight increase. Warming temperatures in the northern Rocky Mountains is associated with earlier spring snow melt, warmer summers, and longer growing seasons (Romme and Turner, 2015). Spring and summer temperatures will rise 8-10°F by mid-century, with increased frequency of hot, dry summers (Westerling et al., 2011). Snowpacks in the GYA have consistently declined due to increased temperatures, and a long-term forecast in the GYA calls for less snow (Tercek et al., 2015). This conclusion is based on analyses showing that temperature increases are the primary cause of decreased snowpack and that temperatures are continuing to trend upward. Another projection calls for a 32% reduction in snowpack in areas typical of elk habitats at mid-elevations and a 56% reduction at higher elevations (Lapp et al., 2005; Creel and Creel, 2009).

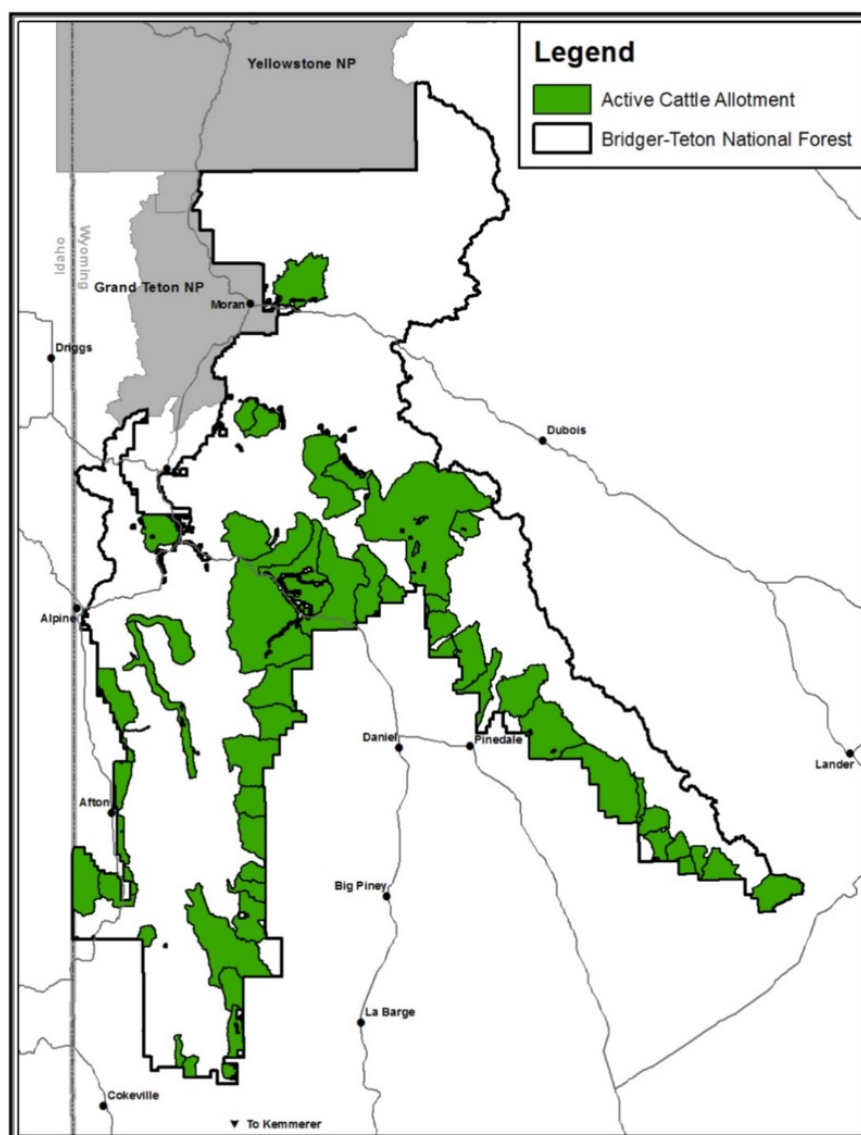


FIGURE 2-14 Active U.S. Forest Service grazing allotments in Bridger-Teton National Forest. SOURCE: Data provided by USFS and BTNF.

Geographic Scope of Populations and Disease and Change in Land Use

Reduced winter snowpack will affect elk and bison by increasing winter forage intake and by causing spring snowmelt and green-up to occur earlier. Reduced snowpack may also reduce the energetic costs of foraging and traveling in winter. As a result of greater forage intake and reduced stress, population growth rates are likely to increase. An empirical elk population model predicted that warmer winters could raise equilibrium population size in Rocky Mountain National Park elk by 50%-100% depending on whether summers are drier or wetter (Wang et al., 2002). Using an empirical population model driven by climate model outputs, it is predicted that Montana elk populations will increase substantially due to reduced snowpack (Creel and Creel, 2009).

Similarly, the annual population growth rate of bison in the central YNP herd was negatively correlated with snowpack, but not so for the northern herd; this was likely due to deeper snow at higher elevations in central YNP than in northern YNP (Fuller et al., 2007). As previously discussed in this chapter, bison movements in winter to lower elevations (including areas outside YNP) are driven by a combination of increased animal density and increased snowpack. Thus, it is likely that reduced snowpack will reduce bison outmigration from YNP, but this could be offset by increased population size unless the population is managed. Increased population growth rate could also lead to increased numbers being removed outside the YNP boundary by management actions. Conversely, reduced snowpack will likely cause earlier migrations upslope in the spring due to earlier green-up, resulting in a shorter duration of bison at low elevations outside YNP.

Temperature and precipitation interactively affect plant growth and thus forage availability. Increased spring temperatures will result in earlier green-up and growth, but increased summer temperatures in water-limited environments can lead to increased evapotranspiration, reduced soil moisture, reduced growth, and earlier curing of forage, which thus results in reduced forage quality. During the dry period of 1989-2009 in the GYA, spring-summer temperatures were warmer and there was reduced spring precipitation, leading to an increased rate and shorter duration of green-up (Westerling et al., 2006; Middleton et al., 2013a). The dry conditions resulted in less green forage and lower pregnancy rate, and a mismatch between time of green forage availability and the period of lactation could also lower recruitment rate, presumably through reduced calf survival (Post and Forchhammer, 2008; Middleton et al., 2013a).

Overall, the positive effects of reduced snowpack and the negative effects of warmer temperatures and increased dryness could counteract one another. The net outcome can most likely be predicted with process-based models. Models of plant growth and snowpack that represent the effects of water, temperature, and snowpack on plant productivity, time of green-up, and time of senescence could be employed to predict future patterns of forage availability seasonally and across the landscape. Such models can be linked to models of animal distributions in response to changing distributions of snow, forage, and land use as well as process-based population dynamics models that consider the effects of forage availability on animal nutritional status and consequent rates of reproduction and survival (e.g., Coughenour, 2005). The implications for brucellosis arise from changes in predicted elk numbers and distributions in relationship to live-stock numbers and potential elk management actions.

7. SUMMARY

With elk now known to be a primary source of *B. abortus* transmission in the GYA, the scope and dynamic complexity of brucellosis in the GYA has expanded. Whereas bison are primarily confined to YNP or just outside its immediate borders, many tens of thousands of elk are spread across a very large and heterogeneous area. Elk are likely a reservoir of brucellosis independent of bison. Elk populations in the GYA have increased for the most part, and elk now occur in larger aggregations than in the past. The change in elk numbers and distributions is in part due to land use changes, including land acquisitions by owners who discourage or prohibit access by hunters, which then creates refugia from hunting offtake and leads to elk aggregations. Also, large numbers of elk continue to be artificially fed in winter in the southern GYA. Despite recognition by management agencies that feeding contributes to *B. abortus* transmission and that it would be desirable to phase out feeding, this goal remains elusive due to extensive habitat overlap with

Revisiting Brucellosis in the Greater Yellowstone Area

livestock operations and questionable assertions that feeding is necessary to maintain abundant elk populations. These major factors have contributed to the sustainability of elk populations as a reservoir for brucellosis.

The bison population has also increased, which has also shifted the distribution of bison across the landscape. Bison are moving from central YNP to northern YNP, and consequently, the northern herd segment has increased in size. Most of the bison exiting YNP do so at the northern boundary, with more exiting when snow is deeper and the population is larger, and there are efforts to manage the bison population through opportunistic removals at the YNP boundary. Northern YNP has shifted from being elk-dominated to bison-dominated. Under the IBMP bison have been successfully contained in designated dispersal areas just outside the YNP boundary. The dispersal area has been enlarged, and bison have also been kept separated from livestock.

REFERENCES

- Barber-Meyer, S.M., L.D. Mech, and P.J. White. 2008. Elk Calf Survival and Mortality Following Wolf Restoration to Yellowstone National Park. Wildlife Monographs 169. The Wildlife Society.
- Barmore, W.J., Jr. 2003. Ecology of Ungulates and Their Winter Range in Northern Yellowstone National Park: Research and Synthesis 1962-1970. Yellowstone Center for Resources. Yellowstone National Park, WY.
- Bienen, L., and G. Tabor. 2006. Applying an ecosystem approach to brucellosis control: Can an old conflict between wildlife and agriculture be successfully managed? *Frontiers in Ecology and the Environment* 4:319-327.
- Bjornlie, D.D., and R.A. Garrott. 2001. Effects of winter road grooming on bison in Yellowstone National Park. *Journal of Wildlife Management* 65:560-572.
- Boyce, M.S. 1989. *The Jackson Elk Herd: Intensive Wildlife Management in North America*. Cambridge, UK: Cambridge University.
- Brennan, A., P.C. Cross, S. Creel, and P. Stephens. 2015. Managing more than the mean: Using quantile regression to identify factors related to large elk groups. *Journal of Applied Ecology* 52:1656-1664.
- Bruggeman, J.E., R.A. Garrott, D.D. Bjornlie, P.J. White, G.R. Watson, and J. Borkowski. 2006. Temporal variability in winter travel patterns of Yellowstone bison: The effects of road grooming. *Ecological Applications* 16:1539-1554.
- Bruggeman, J.E., R.A. Garrott, P.J. White, F.G.R. Watson, and R. Wallen. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications* 17:1411-1423.
- Bruggeman, J.E., P.J. White, R.A. Garrott, and F.G.R. Watson. 2009. Partial migration in central Yellowstone bison. Pp. 217-235 in *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*. R.A. Garrott, P.J.K. White, and F.G.R. Watson, eds. San Diego, CA: Elsevier.
- BLM (Bureau of Land Management). 2014. Grazing Allotment Boundaries. Available online at <https://catalog.data.gov/dataset/grazing-allotment-boundaries> (accessed May 18, 2017).
- Cole, E.K., A.M. Foley, J.M. Warren, B.L. Smith, S.R. Dewey, D.B. Brimeyer, W.S. Fairbanks, H. Sawyer, and P.C. Cross. 2015. Changing migratory patterns in the Jackson elk herd. *Journal of Wildlife Management* 79:877-886.
- Cole, G.F. 1969. *The Elk of Grand Teton and Southern Yellowstone National Parks*. Research Report GRTE-N-1. Washington, DC: National Park Service.
- Coughenour, M.B. 1994. Elk carrying capacity on Yellowstone's northern elk winter range: Preliminary modeling to integrate climate, landscape, and elk nutritional requirements. Pp. 97-112 in *Plants and Their Environments: Proceedings of the First Biennial Scientific Conference on the Greater Yellowstone Ecosystem*, September 16-17, 1991, Mammoth Hot Springs. D. Despain, ed. Technical Report NPS/NRYELL.NRTR-93/XX. USDI/NPS. Denver, CO: U.S. National Park Service, Natural Resources Publication Office.
- Coughenour, M.B. 2005. *Spatial-dynamic Modeling of Bison Carrying Capacity in the Greater Yellowstone Ecosystem: A Synthesis of Bison Movements, Population Dynamics, and Interactions with Vegetation*. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
- Coughenour, M.B., and F.J. Singer. 1996. Yellowstone elk population responses to fire: A comparison of landscape carrying capacity and spatial-dynamic ecosystem modeling approaches. Pp. 169-180 in *The Ecological Implications of Fire in Greater Yellowstone*. J. Greenlee, ed. Fairfield, WA: International Association of Wildland Fire.

Geographic Scope of Populations and Disease and Change in Land Use

- Creel, S., and M. Creel. 2009. Density dependence and climate effects in Rocky Mountain elk: An application for regression with instrumental variables for population time series with sampling error. *Journal of Animal Ecology* 78:1291-1297.
- Creel, S., and J.A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181-1189.
- Cromley, C. 2000. Historical elk migrations around Jackson Hole, Wyoming. Pp. 53-65 in *Developing Sustainable Management Policy for the National Elk Refuge, Wyoming*. T. W. Clark, D. Casey, and A. Halverson, eds. Yale School of Forestry and Environmental Studies Bulletin 104. New Haven, CT: Yale University.
- Cross, P. 2013. Northern Yellowstone Cooperative Wildlife Working Group 2012 Annual Report (October 1, 2012-September 30, 2012). Available online at <http://www.fedgycc.org/wp-content/uploads/2015/06/2012NYCWWGFnlRpt.pdf> (accessed January 4, 2017).
- Cross, P.C., D.M. Heisey, B.M. Scurlock, W.H. Edwards, M.R. Ebinger, and A. Brennan. 2010a. Mapping brucellosis increases relative to elk density using hierarchical Bayesian models. *PLOS ONE* 5:e10322.
- Cross, P.C., E.K. Cole, A.P. Dobson, W.H. Edwards, K.L. Hamlin, G. Luikart, A.D. Middletown, B.M. Scurlock, and P.J. White. 2010b. Probable causes of increasing brucellosis in free-ranging elk of the greater Yellowstone ecosystem. *Ecological Applications* 20:278-288.
- Cross, P.C., E.J. Maichak, A. Brennan, B.M. Scurlock, J. Henningsen, and G. Luikart. 2013. An ecological perspective on *Brucella abortus* in the western United States. *Revue Scientifique et Technique Office International des Epizooties* 32:79-87.
- Cureton, D., and M. Drew. 2015. Brucellosis and Elk in Idaho. Presentation at the Second Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Moran, MT.
- Eberhart, L.L., P.J. White, R.A. Garrott, and D.B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. *Journal of Wildlife Management* 71:594-602.
- Evans, S.B., L.D. Mech, P.J. White, and G.A. Sargeant. 2006. Survival of adult female elk in Yellowstone following wolf recovery. *Journal of Wildlife Management* 70:1372-1378.
- Foley, A.M., P.C. Cross, D.A. Christianson, B.M. Scurlock, and S. Creel. 2015. Influences of supplemental feeding on winter elk calf:cow ratios in southern Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 79:887-897.
- Forristal, V.E., S. Creel, M.L. Taper, B.M. Scurlock, and P.C. Cross. 2012. Effects of supplemental feeding and aggregation on fecal glucocorticoid metabolite concentrations in elk. *Journal of Wildlife Management* 76:694-702.
- French, B. 2016. Landowners southeast of Red Lodge will get help keeping elk away. *Billings Gazette*, October 14, 2016.
- Fuller, J.A., R.A. Garrott, and P.J. White. 2007. Emigration and density dependence in Yellowstone bison. *Journal of Wildlife Management* 71:1924-1933.
- Garrott, R.A., L.L. Eberhardt, P.J. White, and J. Rotella. 2003. Climate-induced variation in vital rates of an unharvested large-herbivore population. *Canadian Journal of Zoology* 81:33-45.
- Garrott, R.A., J.A. Gude, E.J. Bergman, C. Gower, P.J. White, and K.L. Hamlin. 2005. Generalizing wolf effects across the Greater Yellowstone Area: A cautionary note. *Wildlife Society Bulletin* 33:1245-1255.
- Garrott, R.A., P.J. White, and J. Rotella. 2009. The Madison headwaters elk herd: Stability in an inherently variable environment. Pp. 191-216 in *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*. R.A. Garrott, P.J. White, and F.G.R. Watson, eds. San Diego, CA: Elsevier.
- Gates, C.C., B. Stelfox, T. Muhly, T. Chowns, and R.J. Hudson. 2005. *The Ecology of Bison Movements and Distribution in and Beyond Yellowstone National Park*. Calgary, Alberta, Canada: University of Calgary.
- Geremia, C., P.J. White, R.A. Garrott, R. Wallen, K.E. Aune, J. Treanor, and J.A. Fuller. 2009. Demography of central Yellowstone bison: Effects of climate, density, and disease. Pp. 255-279 in *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*. R.A. Garrott, P.J. White, and F.G.R. Watson, eds. San Diego, CA: Elsevier.
- Geremia, C., P.J. White, R.L. Wallen, F.G.R. Watson, J.J.J. Treanor, J. Borkowski, C.S. Potter, and R.L. Crabtree. 2011. Predicting bison migration out of Yellowstone National Park using Bayesian models. *PLOS ONE* 6(2):e16848.
- Geremia, C., R. Wallen, and P. J. White. 2014a. Spatial Distribution of Yellowstone Bison-Winter 2015. National Park Service, Yellowstone National Park, Mammoth, WY. September 2014. Available online at http://www.ibmp.info/Library/OpsPlans/BisonPopulationDiseaseModel_Final_Winter2015.pdf (accessed May 25, 2017).

Revisiting Brucellosis in the Greater Yellowstone Area

- Geremia, C., R. Wallen, and P. J. White. 2014b. Population Dynamics and Adaptive Management of Yellowstone Bison, August 5, 2014. National Park Service, Yellowstone National Park, Mammoth, Wyoming. Available online at http://www.ibmp.info/Library/OpsPlans/2016_BisonRemovalRecommendations_NPS.pdf (accessed May 25, 2017).
- Gude, P.H., A.J. Hansen, R. Rasker, and B. Maxwell. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. *Landscape and Urban Planning* 77:131-151.
- Gude, P.H., A.J. Hansen, and D.A. Jones. 2007. Biodiversity consequences of alternative future land use scenarios in Greater Yellowstone. *Ecological Applications* 17:1004-1018.
- Haggerty, J.H., and W.R. Travis. 2006. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 37:816-830.
- Hamlin, K.L., and J.A. Cunningham. 2009. Monitoring and Assessment of Wolf-ungulate Interactions and Population Trends within the Greater Yellowstone Area, Southwestern Montana, and Montana Statewide. Final Report. Montana Department of Fish, Wildlife, and Parks, Wildlife Division, Helena, MT.
- Haroldson, M.A. 2006. Unduplicated females. Pp. 11-16 in *Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team*, 2005. C.C. Schwartz, M.A. Haroldson, and K. West, eds. Bozeman, MT: U.S. Geological Survey. Available online at <http://www.arlis.org/docs/vol1/B/4845264/4845264-2005.pdf> (accessed January 4, 2017).
- Haroldson, M.A. 2007. Unduplicated females. Pp. 8-11 in *Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team*, 2006. C.C. Schwartz, M.A. Haroldson, and K. West, eds. Bozeman, MT: U.S. Geological Survey. Available online at <http://www.arlis.org/docs/vol1/B/4845264/4845264-2006.pdf> (accessed January 4, 2017).
- Haroldson, M.A. 2008. Assessing trend and estimating population size from count of unduplicated female. Pp. 9-14 in *Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team*, 2007. C.C. Schwartz, M.A. Haroldson, and K. West, eds. Bozeman, MT: U.S. Geological Survey.
- Harris, R.B., G.C. White, C.C. Schwartz, M.A. Haroldson. 2007. Population growth of Yellowstone grizzly bears: Uncertainty and future monitoring. *Ursus* 18:168-178.
- Hobbs, N.T., G. Wockner, F.J. Singer, G. Wang, L. Zeigenfuss, P. Farnes, and M. Coughenour. 2003. Assessing Management Alternatives for Ungulates in the Greater Teton Ecosystem Using Simulation Modeling. Final Report to U.S. Geological Survey, Fort Collins, by Natural Resource Ecology Laboratory, Colorado State University.
- Houston, D.B. 1982. *The Northern Yellowstone Elk Herd*. New York: Macmillan.
- Jimenez, M.D., and S.A. Becker, eds. 2015. *Northern Rocky Mountain Wolf Recovery Program 2014 Interagency Annual Report*. U.S. Fish and Wildlife Service, Idaho Department of Fish and Game, Montana Fish, Wildlife, and Parks, Wyoming Game and Fish Department, Nez Perce Tribe, National Park Service, Blackfoot Nation, Confederated Salish and Kootenai Tribes, Wind River Tribes, Confederated Colville Tribes, Spokane Tribe of Indians, Washington Department of Fish and Wildlife, Oregon Department of Fish and Wildlife, Utah Department of Natural Resources, and USDA Wildlife Services. Helena, MT: USFWS, Ecological Services.
- Jones, J.D., M.J. Kauffman, K.L. Monteith, B.M. Scurlock, S.E. Albeke, and P.C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. *Ecological Applications* 24:1769-1779.
- Kauffman, M., K. Boroff, D. Peck, B. Scurlock, W. Cook, J. Logan, T. Robinson, and B. Schumaker. 2013. Cost-benefit Analysis of a Reduction in Elk Brucellosis Seroprevalence in the Southern Greater Yellowstone Area. University of Wyoming, Laramie, WY.
- Kilpatrick, A.M., C.M. Gillin, and P. Daszak. 2009. Wildlife-livestock conflict: The risk of pathogen transmission from bison to cattle outside Yellowstone National Park. *Journal of Applied Ecology* 46:476-485.
- Lapp, S., J. Byrne, I. Townshend, and S. Kienzie. 2005. Climate warming impacts on snowpack accumulation in an alpine watershed. *International Journal of Climatology* 25:521-536.
- Littell, J.S., M.M. Elsner, G.S. Mauger, E. Lutz, A.F. Hamlet, and E. Salathé. 2011. Regional Climate and Hydrologic Change in the Northern US Rockies and Pacific Northwest: Internally Consistent Projections of Future Climate for Resource Management. Project report: April 17, 2011. Available online at http://cses.washington.edu/picea/USFS/pub/Littell_etal_2010/Littell_etal_2011_Regional_Climatic_And_Hydrologic_Change_USFS_USFWS_JVA_17Apr11.pdf (accessed January 5, 2017).
- Lubow, B., and B. Smith. 2004. Population dynamics of the Jackson elk herd. *Journal of Wildlife Management* 68:810-829.
- MacNulty, D. 2015. Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 1-2, 2015, Bozeman, MT.

Geographic Scope of Populations and Disease and Change in Land Use

- Mao, J.S., M.S. Boyce, D.W. Smith, F.J. Singer, D.J. Vales, J.M. Vore, and E.H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691-1707.
- McIntyre, C., and C. Ellis. 2011. Landscape Dynamics in the Greater Yellowstone Area. Natural Resource Technical Report NPS/GRYN/NRTR-2011/506. Fort Collins, CO: National Park Service.
- MDFWP (Montana Department of Fish, Wildlife & Parks). 2004. Montana Statewide Elk Management Plan. Helena, MT: Montana Department of Fish, Wildlife & Parks.
- MDFWP. 2016. Montana Statewide Elk Management. Available online at <http://fwp.mt.gov/fishandwildlife/management/elk> (accessed April 19, 2016).
- Meagher, M. 1989. Range expansion by bison of Yellowstone National Park. *Journal of Mammalogy* 70:670-675.
- Meagher, M.M. 1993. Winter Recreation-induced Changes in Bison Numbers and Distributions in Yellowstone National Park. Yellowstone National Park, WY.
- Middleton, A.D., M.J. Kauffman, D.E. McWhirter, J.G. Cook, R.C. Cook, A.A. Nelson, M.D. Jimenez, and R.W. Klaver. 2013a. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk herd. *Ecology* 94:1245-1256.
- Middleton, A., D., M.J. Kauffman, D.E. McWhirter, M.D. Jimenez, R.C. Cook, J.G. Cook, S.E. Albeke, H. Sawyer, and P.J. White. 2013b. Linking anti-predator behavior and prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecological Letters* 16:1023-1030.
- Middleton, A.D., T.A. Morrison, J.K. Fortin, C.T. Robbins, K.M. Proffitt, P.J. White, D.E. McWhirter, T.M. Koel, D.G. Brimeyer, W.S. Fairbanks, and M.J. Kauffman. 2013c. Grizzly bear predation links the loss of native trout to the demography of migratory elk in Yellowstone. *Proceedings of the Royal Society B* 280:20130870.
- Murie, O.J. 1951. *The Elk of North America*, 1st ed. Harrisburg, PA: The Stackpole Co.
- NASS (National Agricultural Statistics Service). 2011. Wyoming Agricultural Statistics 2010. Available online at http://www.nass.usda.gov/Statistics_by_State/Wyoming/Publications/Annual_Statistical_Bulletin/bulletin2010.pdf.
- National Geographic. 2016. Special Poster: Yellowstone Elk Migrations, Supervolcano. 229(5). Available online at <http://www.nationalgeographic.com/magazine/2016/05/yellowstone-national-parks-elk-migration-map> (accessed May 22, 2017).
- Northern Rockies Adaptation Partnership. 2014. Northern Rockies Adaptation Partnership: Climate Projections. Available online at http://adaptationpartners.org/nrap/docs/NRAP_climate_projections.pdf (accessed January 5, 2017).
- Olexa, E.M., and P.J.P. Gogan. 2007. Spatial Population structure of Yellowstone bison. *Journal of Wildlife Management* 71(5):1531-1538.
- Owen-Smith, R.N., ed. 1983. *Management of Large Mammals in African Conservation Areas*. Pretoria, South Africa: HAUM Educational.
- Plumb, G.E., P.J. White, M.B. Coughenour, and R.L. Wallen. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. *Biological Conservation* 142:2377-2387.
- Post, E., and M.C. Forchhammer. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. *Philosophical Transactions of the Royal Society B* 363:2367-2373.
- Proffitt, K.M., J.A. Gude, K.L. Hamlin, R.A. Garrott, J.A. Cunningham, and J.L. Grigg. 2010a. Elk distribution and spatial overlap with livestock during the brucellosis transmission risk period. *Journal of Applied Ecology* 48:471-478.
- Proffitt, K.M., J.L. Grigg, R.A. Garrott, K.L. Hamlin, J. Cunningham, J.A. Gude, and C. Jourdonnais. 2010b. Changes in elk resource selection and distributions associated with a late-season elk hunt. *Journal of Wildlife Management* 74:210-218.
- Proffitt, K.M., N. Anderson, P. Lukacs, M.M. Riordan, J.A. Gude, and J. Shamhart. 2015. Effects of elk density on elk aggregation patterns and exposure to brucellosis. *Journal of Wildlife Management* 79:373-383.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Romme, W.H., and M.G. Turner. 2015. Ecological implications of climate change in Yellowstone: Moving into uncharted territory? *Yellowstone Science* 23:6-13.
- Schumaker, B.A., D.E. Peck, and M.E. Kauffman. 2012. Brucellosis in the Greater Yellowstone area: Disease management at the wildlife-livestock interface. *Human-Wildlife Interactions* 6:48-63.
- Schwartz, C.C., M.A. Haroldson, G.C. White, R.B. Harris, S. Cherry, K.A. Keating, D. Moody, and C. Servheen. 2006. Temporal, spatial, and environmental influences on the demographics of grizzly bears in the Greater Yellowstone Ecosystem. *Wildlife Monographs* 161:1-68.

Revisiting Brucellosis in the Greater Yellowstone Area

- Schwartz, C.C., M.A. Haroldson, and K. West, eds. 2009. Yellowstone Grizzly Bear Investigations: Annual Report of the Interagency Grizzly Bear Study Team, 2008. Bozeman, MT: U.S. Geological Survey.
- Singer, F.J., A. Harting, K.K. Symonds, and M.B. Coughenour. 1997. Density dependence, compensation, and environmental effects on elk calf mortality in Yellowstone National Park. *Journal of Wildlife Management* 61:12-25.
- Smith, B.L., and S.H. Anderson. 1996. Patterns of neonatal mortality of elk in northwest Wyoming. *Canadian Journal of Zoology* 74:1229-1237.
- Smith, B.L., and S.H. Anderson. 1998. Juvenile survival and population regulation of the Jackson elk herd. *Journal of Wildlife Management* 62:1036-1045.
- Smith, B.L., and S.H. Anderson. 2001. Does dispersal help regulate the Jackson herd? *Wildlife Society Bulletin* 29:331-342.
- Smith, D.W., T.D. Drummer, K.M. Murphy, D.S. Guernsey, and S.B. Evans. 2004. Winter prey selection and estimation of wolf kill rates in Yellowstone National Park, 1995-2000. *Journal of Wildlife Management* 68:153-166.
- Taper, M.L., and P.J.P. Gogan. 2002. The northern Yellowstone elk: Density dependence and climatic conditions. *Journal of Wildlife Management* 66:106-122.
- Tereck, M., A. Rodman, and D. Thoma. 2015. Trends in Yellowstone's snowpack. *Yellowstone Science* 23:20-27.
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2014. Brucellosis Regionalization Risk Assessment Model: An Epidemiologic Model to Evaluate the Risk of *B. abortus* Infected Undetected Breeding Cattle Moving out of the Designated Surveillance Areas in Idaho, Montana, and Wyoming. Fort Collins, CO: Center for Epidemiology and Animal Health. December 2014. 54 pp.
- USFS (U.S. Forest Service). 2008. Rocky Mountain Region GIS Data Library—Region Wide Datasets. Available online at <https://www.fs.usda.gov/detail/r2/landmanagement/gis/?cid=stelprdb5165938> (accessed May 18, 2017).
- USFS. 2009. Range Allotment Boundaries for the Northern Region. Available online at https://www.fs.usda.gov/detailfull/r1/landmanagement/gis/?cid=fsp5_031000&width=full (accessed May 18, 2017).
- USFS. 2015. Intermountain Region GIS Data Library. Available online at <https://www.fs.usda.gov/main/r4/landmanagement/gis> (accessed May 18, 2017).
- USFWS (U.S. Fish & Wildlife Service). 2016. Draft 2016 Conservation Strategy for the Grizzly Bear in the Great Yellowstone Ecosystem. Available online at <https://www.fws.gov/mountain-prairie/es/grizzlyBear.php> (accessed January 5, 2017).
- USFWS and NPS (U.S. Fish & Wildlife Service and National Park Service). 2007. Bison and Elk Management Plan for the National Elk Refuge and Grand Teton National Park. Available online at <https://www.fws.gov/bisonandelkplan> (accessed January 5, 2017).
- Varley, N., and M.S. Boyce. 2006. Adaptive management for reintroductions: updating a wolf recover model for Yellowstone National Park. *Ecological Modelling* 193:315-339.
- Vucetich, J.A., D.W. Smith, and D.R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos* 111:259-270.
- Wallen, R.L., P.J. White, and C. Geremia. 2015. Historical perspective—from near eradication to livestock to wildlife. Chapter 3 in *Yellowstone Bison: Conserving an American Icon in Modern Society*. P.J. White, R.L. Wallen, and D.E. Hallac, eds. Yellowstone Association: Yellowstone National Park.
- Wang, G., N.T. Hobbs, F.J. Singer, D. S. Ojima, and B.C. Lubow. 2002. Impacts of climate changes on elk population dynamics in Rocky Mountain National Park, Colorado, U.S.A. *Climatic Change* 54:205-223.
- Westerling, A.L., H.G. Hidalgo, D.R. Cayan, and T.W. Swetnam. 2006. Warming and earlier spring increase western U.S. forest wildfire activity. *Science* 313:940-943.
- Westerling A.L., M.G. Turner, E.A.H. Smithwick, W.H. Romme, and M.G. Ryan. 2011. Continued warming could transform Greater Yellowstone fire regimes by mid-21st century. *Proceedings of the National Academy of Sciences of the United States of America* 108(32):13165-13170.
- WGFC (Wyoming Game and Fish Commission). 2007. Final Wyoming Gray Wolf Management Plan. Available online at <https://www.fws.gov/mountain-prairie/species/mammals/wolf/WolfFinal2007WyomingGrayWolfManagementPlan.pdf> (accessed January 5, 2017).
- WGFD (Wyoming Game & Fish Department). 2011. Brucellosis Management Action Plan Updates. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed January 5, 2017).
- WGFD. 2014. 2014 Big Game Job Completion Reports. Available online at <https://wgfd.wyo.gov/Hunting/Job-Completion-Reports> (accessed May 25, 2017).

Geographic Scope of Populations and Disease and Change in Land Use

- White, P.J., and R.A. Garrott. 2005a. Northern Yellowstone elk after wolf restoration. *Wildlife Society Bulletin* 33:942-955.
- White, P.J., and R.A. Garrott. 2005b. Yellowstone's ungulates after wolves—expectations, realizations, and predictions. *Biological Conservation* 125:141-152.
- White, P.J., R.A. Garrott, and L. L. Eberhardt. 2003. Evaluating the consequences of wolf recovery on Northern Yellowstone Elk. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming, YCR-NR-2004-02.
- White, P.J., R.A. Garrott, S. Cherry, F.G.R. Watson, C.N. Gower, M.S. Becker, and E. Meridith. 2009. Changes in elk resource selection and distribution with the reestablishment of wolf predation risk. Pp. 451-476 in *The Ecology of Large Mammals in Central Yellowstone: Sixteen Years of Integrated Field Studies*. R.A. Garrott, P.J. White, and F.G.R. Watson, eds. San Diego, CA: Elsevier.
- White, P.J., K.M. Proffitt, and T.O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. *American Midland Naturalist* 167:174-187.
- White, P.J., R.A. Garrott, and G.E. Plumb. 2013. Ecological process management. Pp. 3-9 in *Yellowstone's Wildlife in Transition*. P.J. White, R.A. Garrott, and G.E. Plumb, eds. Cambridge, MA: Harvard University Press.
- Wisdom, M.J., and J.G. Cook. 2000. North American elk. Pp. 694-735 in *Ecology and Management of Large Mammals in North America*. S. Demerai, and P.R. Krausman, eds. Upper Saddle River, NJ: Prentice Hall.
- Wright, G.J., R.O. Peterson, D.W. Smith, and T.O. Lemke. 2006. Selection of northern Yellowstone elk by gray wolves and hunters. *Journal of Wildlife Management* 70:1070-1078.

3

Ecology and Epidemiology of *Brucella abortus* in the Greater Yellowstone Ecosystem

1. REVIEW OF BRUCELLOSIS CASES SINCE 1998

At the time of the last National Research Council (NRC) report in 1998, there had been no *Brucella abortus* infected cattle herds detected in the Greater Yellowstone Area (GYA) for several years. Between 2002 and 2016, a total of 22 cattle herds and 5 privately owned bison herds were infected (see Figure 3-1 and Table 3-1). These cases were distributed across all three states in the GYA (Idaho, Montana, and Wyoming), and the number of cases appears to be increasing over time (Cross et al., 2013c). Available field and molecular epidemiologic information on these herds suggests that elk are the most likely source of infection in each of these cases (Rhyan et al., 2013; Kamath et al., 2016).

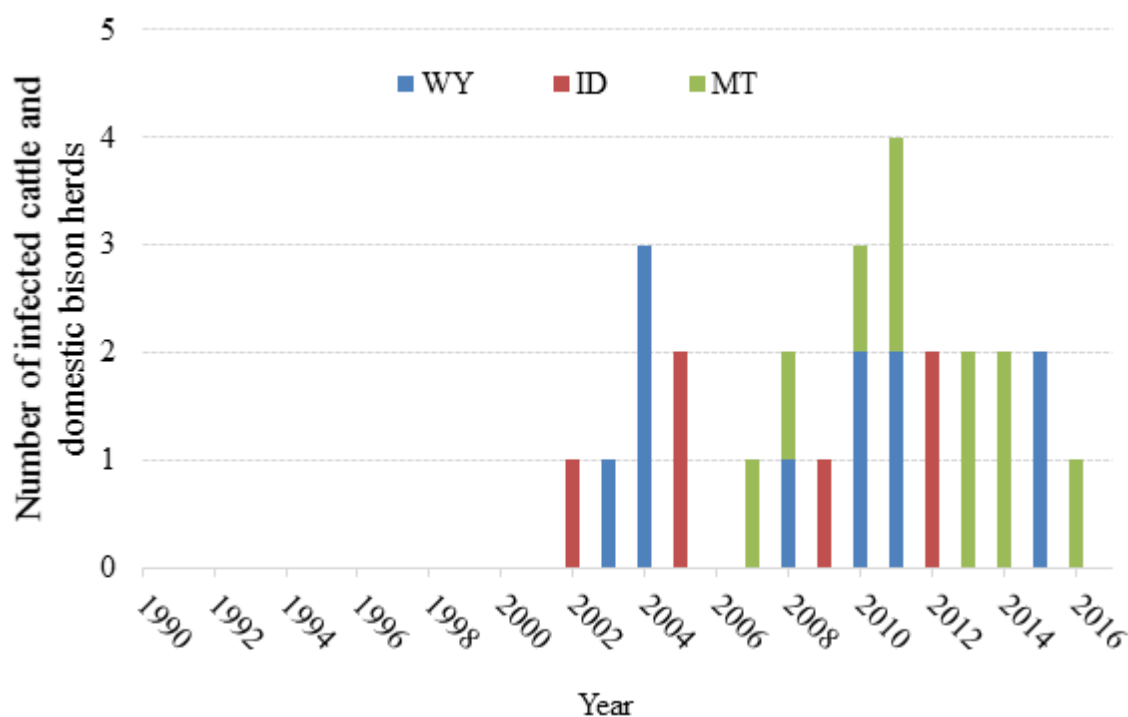


FIGURE 3-1 Number of cattle and domestic bison herds infected with *B. abortus* in the GYA by state from 1990 to 2016.

TABLE 3-1 Brucellosis Herds Detected in the GYA, 2002-2016

State	Month	Year	Herd Type	Herd Size	County	Method of Detection	Disposition	Trace Out States
ID	Apr	2002	Beef cattle	50	Fremont	Herd test conducted due to culture positive elk in the area	Depopulated	ID, NE, WY
	Nov	2005	Beef cattle	Unavailable	Bonneville	MCI trace	Depopulated	CA, CO, ID, MT, NE, UT
	Nov	2005	Beef cattle	60	Butte	Epidemiologic link to Bonneville herd	Depopulated	Unavailable
	Nov	2009	Beef cattle	589	Jefferson	Slaughter surveillance	Partially depopulated	Unavailable
	Apr	2012	Beef cattle	65	Fremont (outside of DSA)	California slaughter trace	Test and remove	AZ, ID, TX, UT
	Mar	2012	Bison	268	Bonneville	DSA related test	Test and remove	ID
MT	May	2007	Beef cattle	260	Park (Carbon)	Pre-interstate shipment test at a livestock auction market. Cow had aborted twice prior to sale	Depopulated	CA, CO, ID, IL, KS, MN, MO, MT, NE, SD, TX, WI, WY
	May	2008	Beef cattle	28	Park	Herd tested as part of MT effort to develop risk mitigation herd plans near Yellowstone National Park	Depopulated	HI, ID, MN, MT, ND, SD, WA, WY
	Nov	2010	Bison	3,250	Gallatin	DSA herd management plan test	Test and remove	CO, ID, KS, MT, NE, SD, TX, WY
	Sep	2011	Beef cattle	275	Park	DSA related movement test	Test and remove	ID, MN, MT, NE, SD, UT, WA
	Nov	2011	Bison	1,550	Madison	Trace herd test due to epidemiological link to the 2010 bison herd	Test and remove	Unavailable
	Sep	2013	Beef cattle	1,500	Madison	DSA related pre-slaughter test of a 2-year-old female	Test and remove	CA, CO, IA, KS, MN, MT, NE, SD
	Oct	2013	Beef cattle	700	Park	Brucellosis certified annual herd test	Test and remove	CA, MN, MT, NE, SD, TX
	Oct	2014	Beef cattle	650	Park/Carbon	DSA related movement test	Test and remove	Pending
	Nov	2014	Beef cattle	2,340	Madison	DSA related movement test	Test and remove	Pending
	Nov	2016	Bison	178	Beaverhead	Voluntary DSA herd test	Test and remove	GA, SD
WY	Nov	2003	Beef cattle	400	Sublette	Slaughter surveillance	Depopulated	Unavailable
	Jan	2004	Beef feedlot	800	Washakie	Trace herd test due to epidemiologic link with the 2003 Sublette County herd	Depopulated	Unavailable
	Jun	2004	Beef cattle	600	Teton	Interstate movement test	Depopulated	CO, ID, KS, MT, NE, SD, TX, WY
	Nov	2004	Beef cattle	800	Teton	Trace herd test, contact with June 2004 Teton County herd	Depopulated	Unavailable

continued

TABLE 3-1 Continued

State	Month	Year	Herd Type	Herd Size	County	Method of Detection	Disposition	Trace Out States
	Jun	2008	Beef cattle	800	Sublette	First-point test at a WY livestock auction market	Depopulated	CA, CO, ID, KS, MN, MT, NE, SD, WY
	Oct	2010	Beef cattle	500	Park	DSA related change of ownership testing at a WY livestock auction market	Test and remove	MT, WY
	Nov	2010	Bison	1,067	Park	DSA related pre-sale movement testing of yearling heifers	Test and remove	CO, MT, NV, WY
	Feb	2011	Beef cattle	500	Park	DSA related movement test at a MT livestock auction market, 5-year-old cull cow	Test and remove	MT
	Jul/Sep	2011	Beef cattle	500	Park	DSA related on-farm, pre-sale test of 13-month-old heifers	Test and remove	Unavailable
	Oct	2015	Beef cattle	515	Park	DSA herd plan test	Test and remove	Unavailable
	Nov	2015	Beef cattle	717	Sublette	DSA herd plan test	Test and remove	CO, WY

*Ecology and Epidemiology of *Brucella abortus* in the Greater Yellowstone Ecosystem*

1.1 Idaho

Between April 2002 and 2012, four cattle herds and one privately owned bison herd in Idaho were infected with brucellosis. Idaho lost Class Free status in January 2006, and a brucellosis action plan was created resulting in Class Free status being regained in July 2007. Due to changes to the federal brucellosis regulations in 2010 relative to the requirements for retention of that status, Idaho has maintained Class Free status despite finding three additional affected herds since 2009, including a Fremont County cattle herd that was located outside of Idaho's designated surveillance area (DSA). No herds remain quarantined for brucellosis as of March 2016.

1.2 Montana

Between May 2007 and November 2016, seven beef cattle herds and three privately owned bison herds were diagnosed with brucellosis in Montana. The infected herds found in 2007 and 2008 were slaughtered with federal indemnity, while all herds identified thereafter have undergone a test-and-remove protocol under state quarantine. The Montana Department of Livestock developed and implemented a Brucellosis Action Plan in May 2009, and the state successfully regained Class Free status in July 2009.

1.3 Wyoming

From 1989 to November 2003, no brucellosis-infected herds were identified in Wyoming; but, between November 2003 and November 2015, 10 cattle herds and 1 domestic bison herd were infected. Wyoming lost Class Free status in 2004, and the Governor of Wyoming appointed a Wyoming Brucellosis Coordination Team to develop a Brucellosis Management Plan. The state regained Class Free status in 2006 and subsequently identified 6 cattle herds and 1 privately owned bison herd as infected with *B. abortus*.

1.4 Impacts Outside the GYA

As a result of the disclosure of brucellosis in cattle and privately owned bison herds, animals that left those herds prior to diagnosis are required to be traced and their disease status investigated. More than 15,000 animals that had left the affected herds were required to be traced, and a number of those animals were found in non-GYA states (see Figure 3-2). The extensive movement of cattle from the DSA has implications for the implementation of the DSA, because it relates to the likelihood of an infected animal moving out of the area as well as the cost of testing to ensure that contact herds remain uninfected.

2. DISEASE DYNAMICS IN BISON AND ELK

As noted in the previous NRC report (1998), wild bison in the GYA have a relatively high seroprevalence of brucellosis. In bison from the National Elk Refuge (NER) in Wyoming, the seroprevalence of brucellosis ranged from 40% to 83% from 2000 to 2008 (mean = 64%, 95% confidence interval [CI] = 0.58, 0.69) (Scurlock and Edwards, 2010). The seroprevalence among adult females is relatively steady over time in Yellowstone National Park (YNP) at 60%, despite large changes in population size (Hobbs et al., 2015). This suggests that the population size of bison may not be a strong determinant of brucellosis transmission rates in bison (Hobbs et al., 2015). By combining serological data with culture results, active infections are more likely among 2- to 4-year-old Yellowstone bison. Older bison, while likely to be seropositive, are less likely to be culture positive (Treanor et al., 2011). However, this does not necessarily mean that those animals are not infected. In chronically infected animals, there are often fewer organisms per gram of tissue, making it more difficult to obtain a positive culture.

Revisiting Brucellosis in the Greater Yellowstone Area

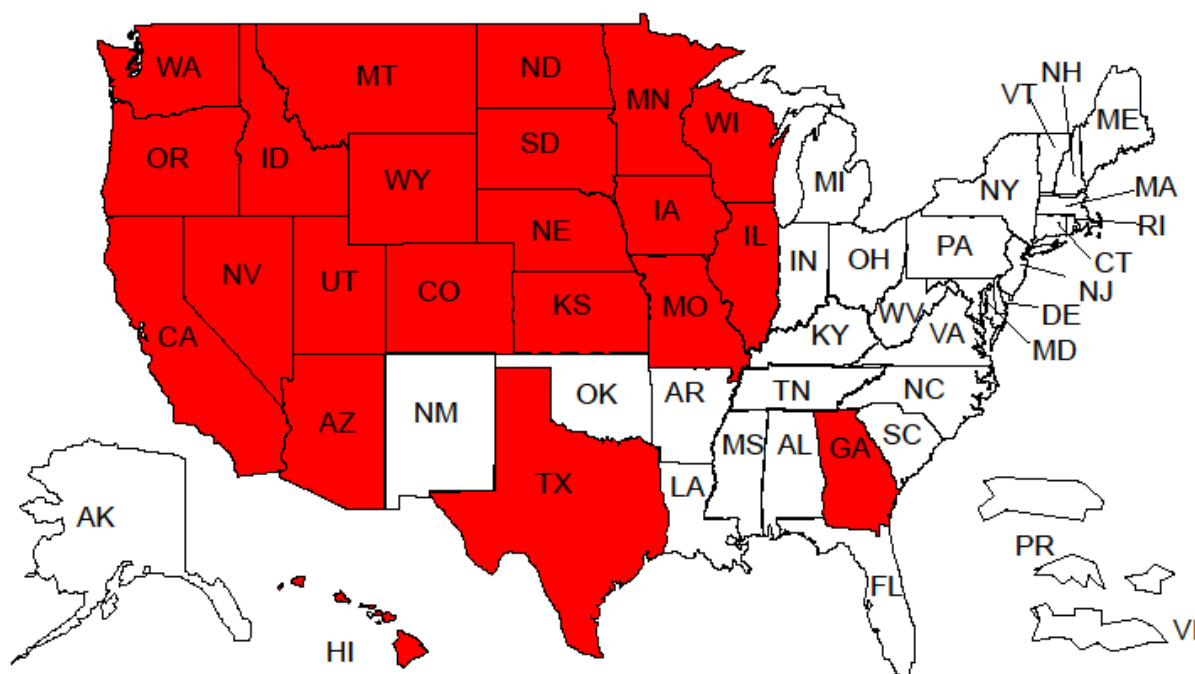


FIGURE 3-2 States to which animals leaving Brucellosis-affected herds in the GYA were traced, 2002-2016.

One of the significant findings of the 1998 NRC report was that “*B. abortus* is unlikely to be maintained in elk if elk winter-feedgrounds were closed.” This was also the consensus of the respondents to the 1998 NRC questionnaire as well as the conclusion of McCorquodale and Digiacomo (1985). This conclusion was due in part to the low seroprevalence in elk anywhere outside of the supplemental feedgrounds prior to 2000 (see Figure 3-3). Data collected after the 1998 NRC report, however, cast this earlier conclusion into doubt, because elk seroprevalence in some management units is now comparable to areas with supplemental feedgrounds (see Figure 3-3). This does not appear to be due to a lack of sampling in areas that were previously at low seroprevalence (see Figure 3-4). While the numbers of samples in any given year may be low, the data, in aggregate, across many years suggest that these increases are not an artifact of sampling error but are consistent changes over a long time period (e.g., see Figures 3-5 and 3-6).

Whole genome sequencing of brucellosis isolates collected from 1985 to 2013 in cattle, elk, and bison across the GYA suggest that brucellosis was introduced into GYA bison and elk on at least five separate occasions, presumably from cattle (Kamath et al., 2016). One of these five lineages is associated with bison within Yellowstone and a few elk isolates from the same area. The *Brucella* isolates from many of the unfed elk in Montana and Wyoming, however, originated from the Wyoming feedgrounds instead of Yellowstone bison. This suggests that control efforts implemented in bison within YNP are unlikely to have any effect on these unrelated lineages in elk populations outside of YNP. Two different lineages were able to move from Wyoming feedgrounds to western Montana, potentially in the 1990s to early 2000s, followed by subsequent local transmission rather than repeated invasions from the feedgrounds (Kamath et al., 2016). This timing is coincident with increases in the seroprevalence in elk in these regions (see Figure 3-5), and it suggests that elk are able to maintain the infection locally after those introductions. The *B. abortus* isolates from elk in the Wiggins Fork region of Wyoming also derive from the feedgrounds, but the extent of local transmission among elk there is less clear as there are a large number of isolates that connect directly back to the feedgrounds rather than other local isolates (Kamath et al., 2016). Finally, genetics data have been used to estimate a diffusion rate of the disease over time, which averaged 3-8 km/yr overall but appeared more recently to be increasing in speed. The two fastest lineages were expanding at a rate of 12 km/yr as of 2013 (Kamath et al., 2016).

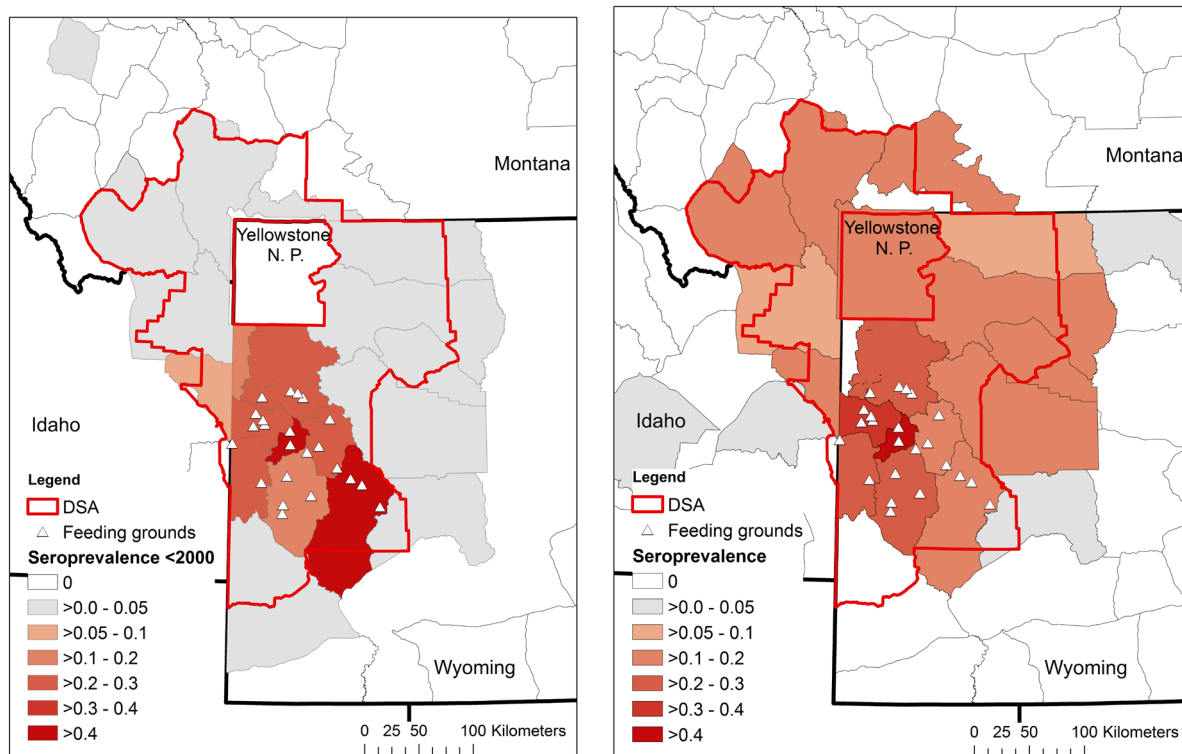
Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

FIGURE 3-3 Maps of seroprevalence in elk using data prior to 2000 (left) and from 2010 to 2015 (right). The designated surveillance area is represented by the red line while the polygons show elk management units. SOURCE: Data provided by the state and federal wildlife agencies of Idaho, Montana, and Wyoming.

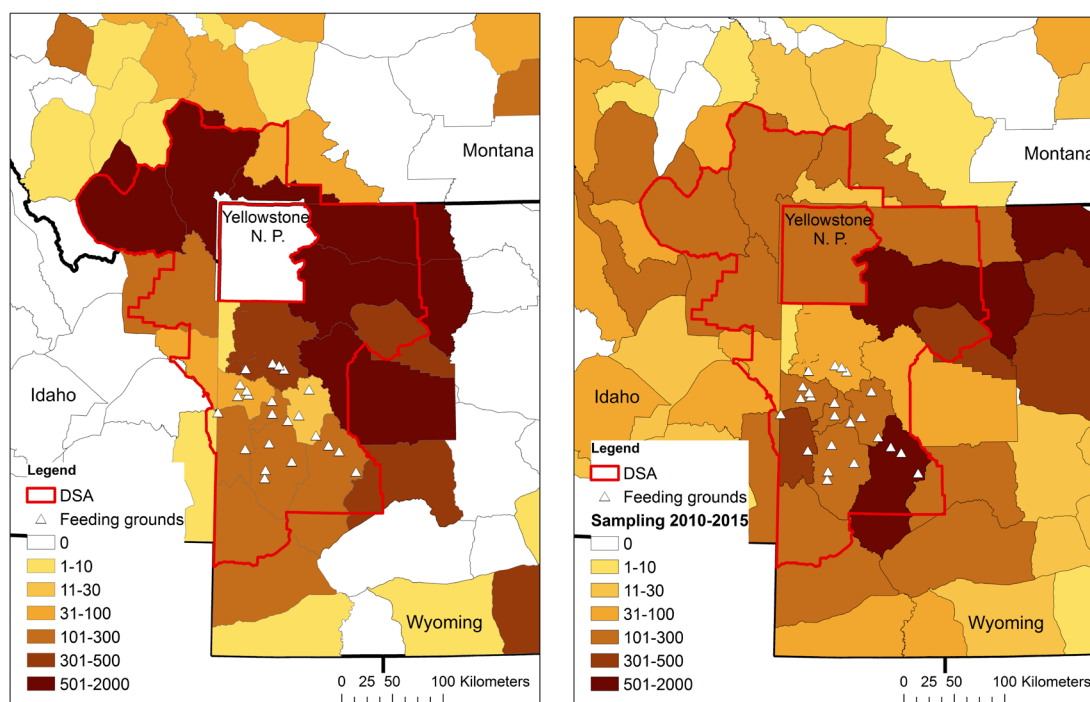


FIGURE 3-4 Maps of sampling effort in elk prior to 2000 (left) and from 2010 to 2015 (right). The designated surveillance area is represented by the red line while the polygons show elk management units. SOURCE: Data provided by the state and federal wildlife agencies of Idaho, Montana, and Wyoming.

Revisiting Brucellosis in the Greater Yellowstone Area

Brucellosis seroprevalence in elk appears to be increasing in several herds in Montana. From 2001-2013, seroprevalence in elk from district 323 was estimated at 28% ($n = 36$, 95% CI = 0.14, 0.45) even though the elk tracking data from that area do not suggest much overlap with either bison or elk from the Wyoming feedgrounds (MDFWP, 2015; Proffitt et al., 2015). More recent testing in the Mill Creek area of Paradise Valley, Montana, showed elk seroprevalence at 53% ($n = 32$, 95% CI = 0.32, 0.68). Montana's elk management units (EMUs) 362 and 313 are two areas where there are sufficient data through time to conclude that the seroprevalence does appear to be increasing (see Figure 3-5).

Several studies have been published on the seroprevalence of brucellosis in Wyoming elk. The seroprevalence in elk on supplemental feedgrounds is strongly correlated with the length of the feeding season, which overlaps with the presumed abortion period in the third trimester of pregnancy (Cross et al., 2007). An increase in the end date of the feeding season is correlated with an increase from 10% to 30% seroprevalence. Furthermore, the end date of the feeding season is highly correlated with the winter snow-pack from one year to the next. Excluding the NER, point estimates of elk population size or density are not significantly associated with seroprevalence. Thus, disease transmission in this system may be driven by an interaction between host density and the timing of disease transmission. Sample testing data from 1993-2009 are aggregated over time for both on and off of supplemental feedgrounds in order to have sufficient sample sizes to make comparisons across regions (Scurlock and Edwards, 2010). However, there is some indication that seroprevalence may be increasing over time in some elk herds (Scurlock and Edwards, 2010). In examining seroprevalence at the broad herd unit scale as well as at the finer hunt area scale, areas south of the feedgrounds with relatively low elk densities did not appear to have any increase in brucellosis (Cross et al., 2010a,b). Most of the observed increases in elk seroprevalence appear to be in the mid-2000s in both Montana and Wyoming (Cross et al., 2010a,b; see Figure 3-6). Meanwhile some regions show no evidence of increasing seroprevalence despite significant sampling efforts and being adjacent to supplemental feedgrounds (see Figure 3-7).

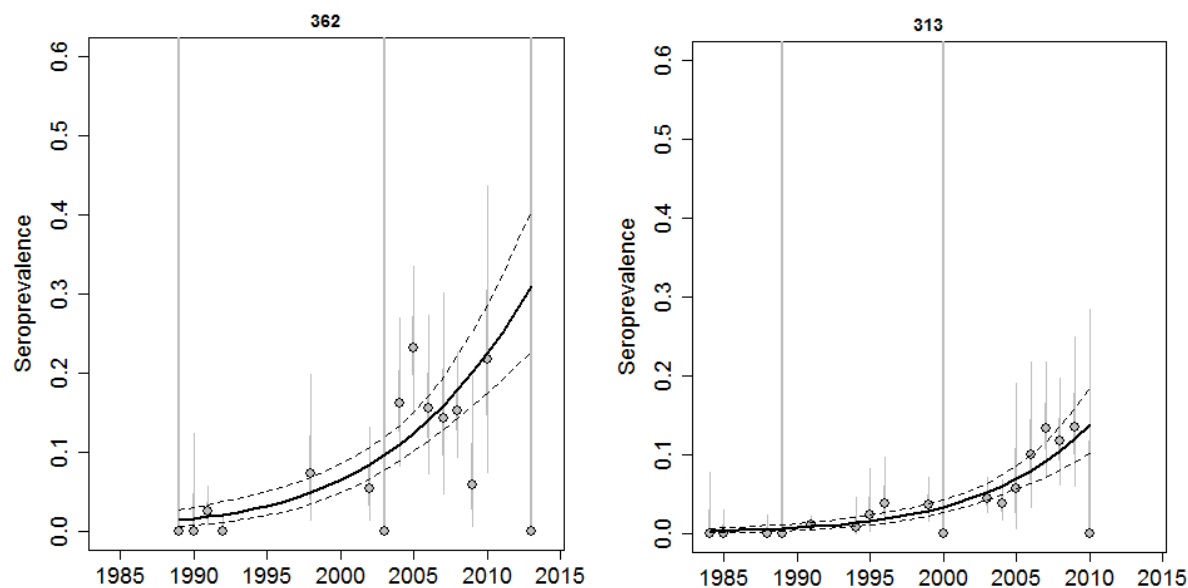


FIGURE 3-5 Elk seroprevalence in the East Madison Hunt District (HD) 362 (left plot) and Gardiner Area HD 313 (right plot). Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Montana Department of Fish, Wildlife & Parks.

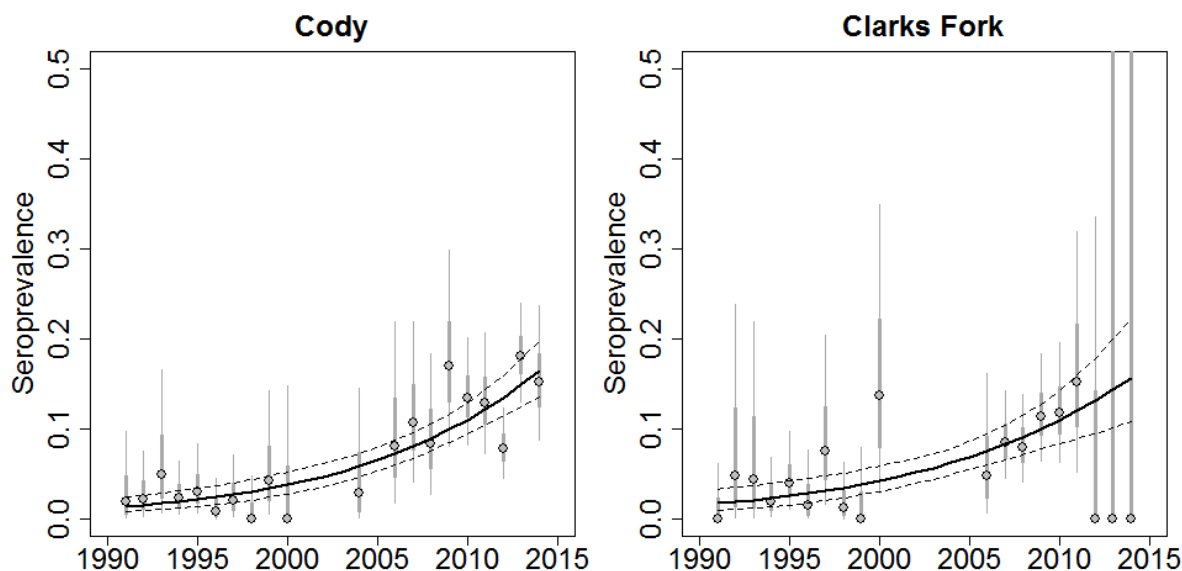
Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

FIGURE 3-6 Elk seroprevalence in the Cody (left plot) and Clarks Fork (right plot) regions of Wyoming. Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Wyoming Game & Fish Department.

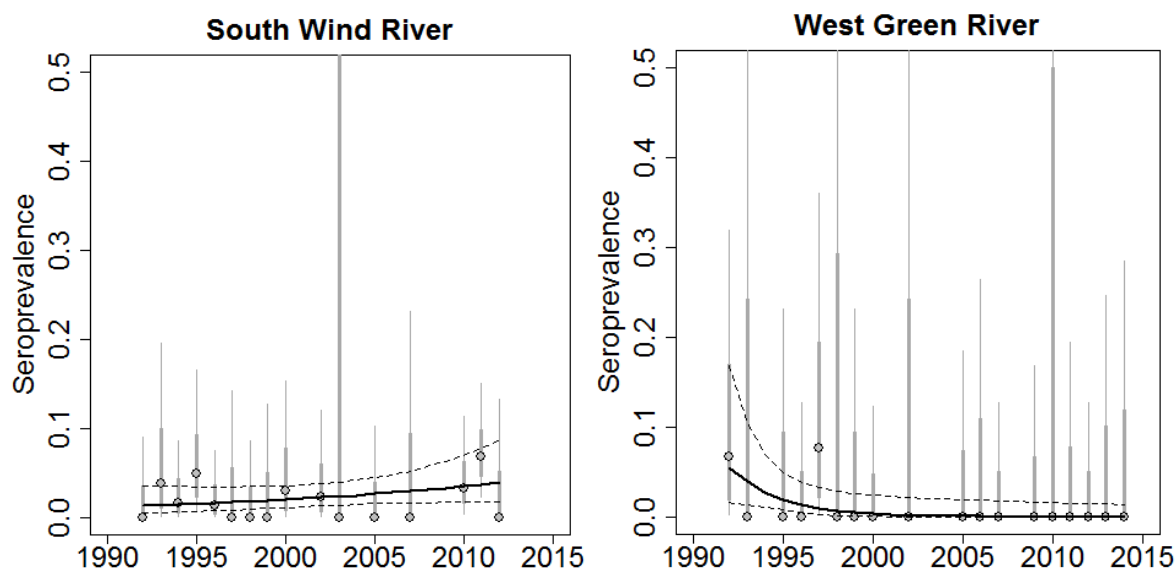


FIGURE 3-7 Elk seroprevalence in the South Wind River (left plot) and West Green River (right plot) regions of Wyoming, both of which are south and adjacent to regions with supplemental feedgrounds. Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Wyoming Game & Fish Department.

Revisiting Brucellosis in the Greater Yellowstone Area

Brucellosis was first observed in Idaho elk in 1998. Prior to 2002, elk seroprevalence was relatively low in all areas tested except Rainey Creek, which was the site of an elk feedground that operated from 1978-2006 and fed between 150 and 600 elk (Etter and Drew, 2006). Since 2002, there have been observed increases in elk seroprevalence in Montana and Wyoming, and although surveillance is being conducted in those areas, there have been no recent studies published using Idaho data aside from Etter and Drew. Data provided to the committee for this review suggest that elk seroprevalence remains low in Districts 66A and 76, which are mostly outside of the DSA (see Figure 3-8). Other regions within the Idaho portion of the DSA appear to have increasing levels of elk seroprevalence (in Districts 61, 62, and 67; see Figure 3-9). Due to the limited sampling in some regions, it is difficult to assess whether the dynamics of brucellosis in some areas are changing (in Districts 64, 65, and 66; see Figure 3-10).

3. EFFECTS OF POPULATION SIZE AND AGGREGATION ON BISON AND ELK TRANSMISSION

To understand the dynamics of infectious diseases and to implement control strategies for effectively addressing brucellosis, it will be important to understand the relationship between host density and parasite transmission (Anderson and May, 1991; McCallum et al., 2001). If transmission and host density are correlated, models predict that the parasite cannot persist below a certain threshold of host density (Kermack and McKendrick, 1927; Getz and Pickering, 1983). This forms the basis for using social distancing (e.g., school closures) to control pandemics (Glass and Barnes, 2007; Cauchemez et al., 2008; Halloran et al., 2008). In natural populations, the distribution and abundance of a host species can be affected by manipulating hunting pressure (Conner et al., 2007), artificial food and water sources (Miller et al., 2003; Rudolph et al., 2006; Cross et al., 2007), and predator distributions (White et al., 2012).

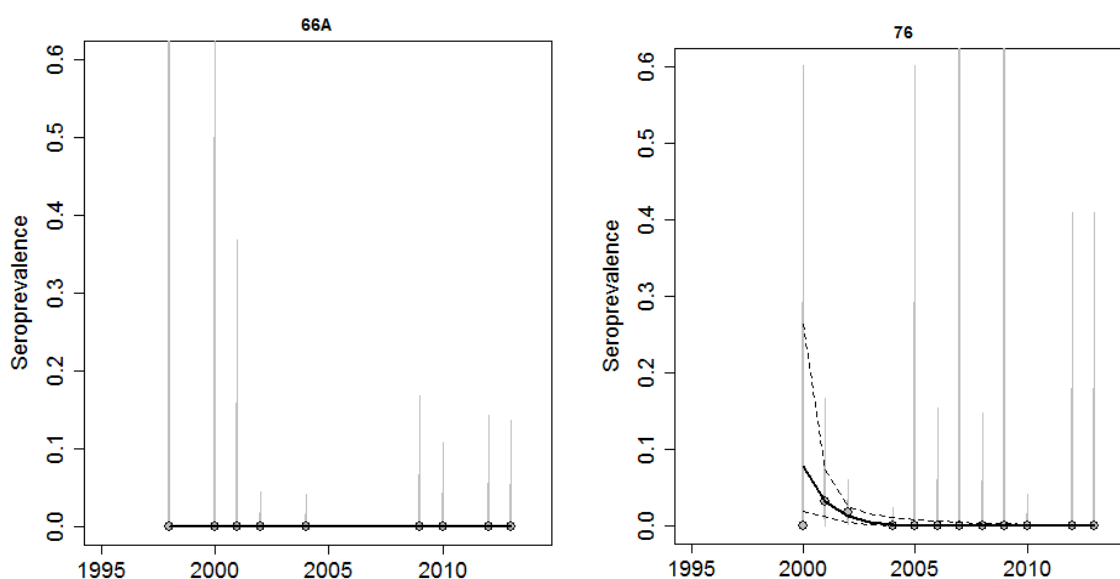


FIGURE 3-8 Elk seroprevalence over time for two management units in Idaho, District 66A (left), District 76 (right). Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Idaho Department of Fish and Game.

Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

For directly transmitted parasites, contact rates may be more related to local measures of host density (i.e., density or number of hosts in a group) rather than broader scale measures (i.e., density of a region with many groups). Furthermore, many ungulate group size distributions, including elk, are highly right-skewed whereby most groups are small, but there are a few very large groups (Cross et al., 2009, 2013c; Brennan et al., 2015). This may result in super-spreader dynamics at the group level whereby a few large groups drive disease dynamics (Lloyd-Smith et al., 2005). This issue has been addressed in human systems under the “core-groups” moniker (e.g., intravenous drug users [see Hethcote, 1978; May and Anderson, 1984; Becker and Dietz, 1995; Dushoff and Levin, 1995]) but it has not had much application to natural populations. In social species like elk and bison, management approaches that alter group size distributions may be more effective at reducing disease transmission than lowering overall population densities.

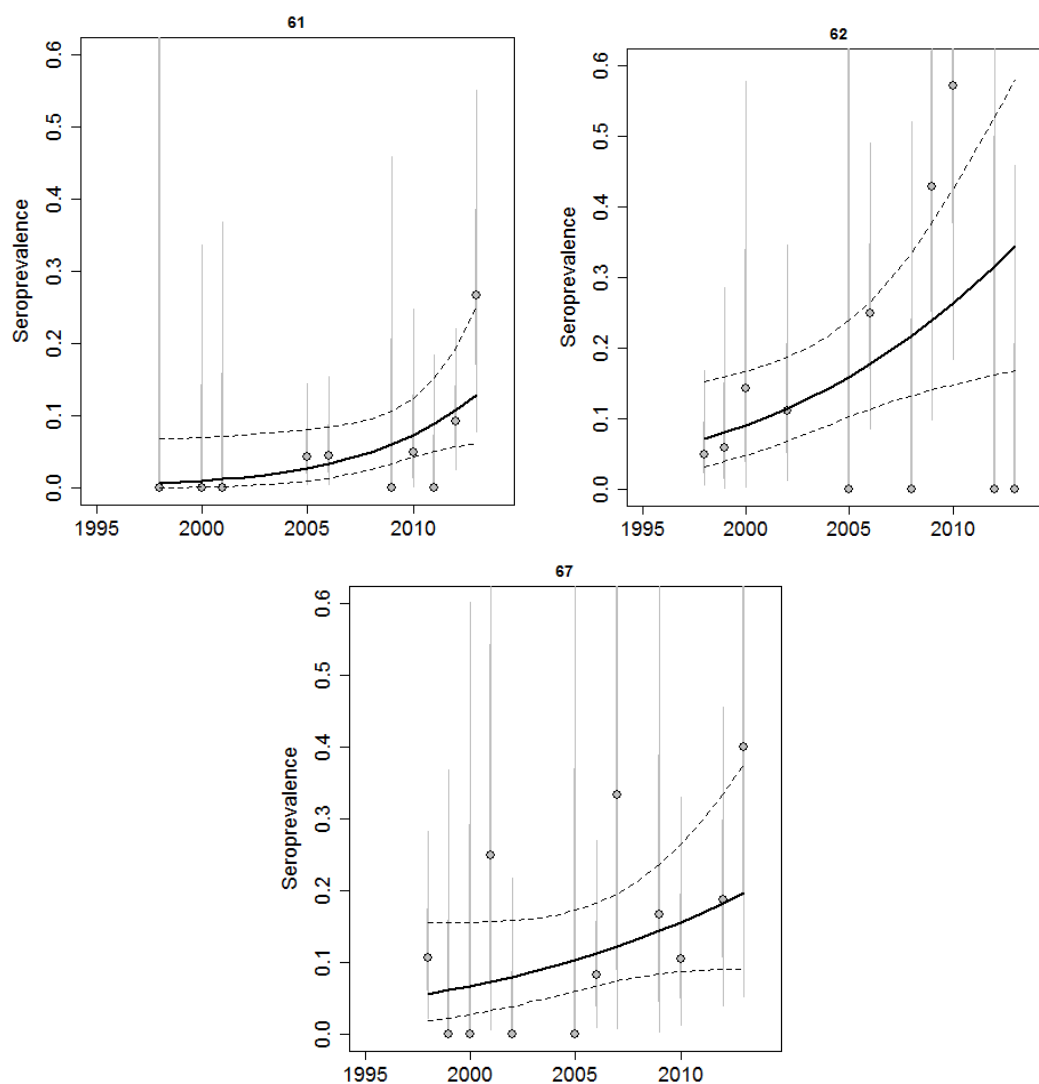


FIGURE 3-9 Elk seroprevalence over time for management units in Idaho where the seroprevalence may be increasing (Districts 61, 62, and 67). Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Idaho Department of Fish and Game.

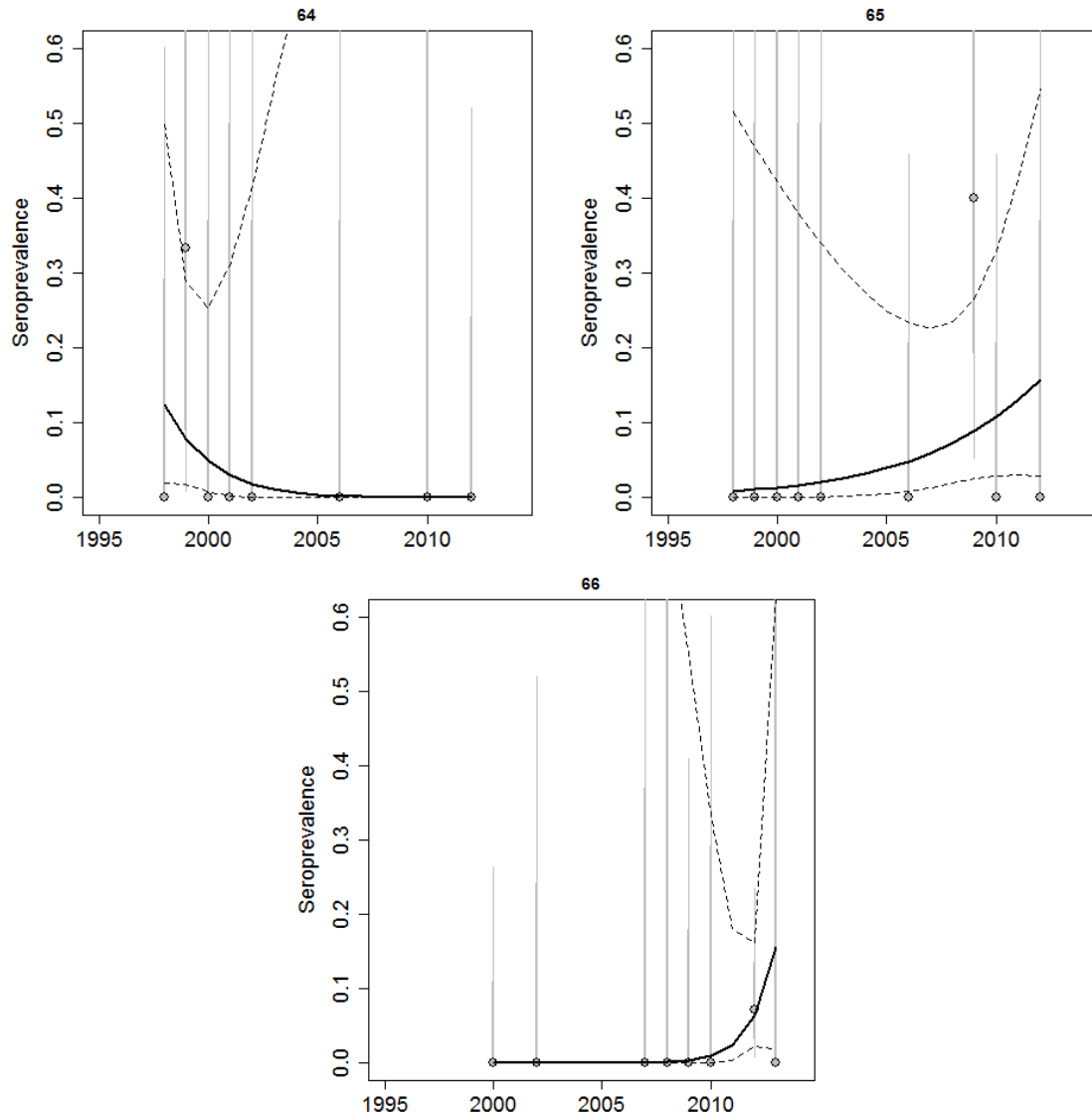
Revisiting Brucellosis in the Greater Yellowstone Area

FIGURE 3-10 Elk seroprevalence over time for several management units in Idaho (Districts 64, 65, and 66) that are too weakly sampled to assess any temporal trends. Each point represents the raw seroprevalence for that year. Thick and thin gray error bars on each point represent the 50% and 95% confidence intervals on that estimate. The black line represents the temporal trend as estimated from a linear time trend in a logistic regression. Dotted lines are the 95% confidence interval on the predicted seroprevalence using a quasibinomial error distribution. SOURCE: Data courtesy of Idaho Department of Fish and Game.

There are a number of scientific challenges involved in relating host density to disease transmission. First, transmission is not directly observable; therefore, seroprevalence is often used as a surrogate. However, exposure could have occurred anytime from birth to the sampling date. Meanwhile, individual elk shift among groups relatively frequently. This makes it difficult to relate serology to group size metrics (Cross et al., 2013a). Second, it is unclear what the denominator should be when calculating elk density. Cross and colleagues investigated the relationship between the rate of increase in elk seroprevalence and elk density at the broad herd unit scale (2010a) as well as the finer hunt area scale (2010b). In both cases, the area used in the calculation of elk density was the total area of the management unit, which probably includes a large amount of area that is not elk habitat. By further investigating multiple different metrics of

Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

elk density, Brennan and colleagues (2014) found that while all the springtime elk density metrics were correlated with the increases in brucellosis, there was not one particular metric of elk density that did much better than the others. Third, elk population size, density, and seroprevalence are factors that change over time, and seroprevalence is likely to respond to changes in elk density at a lag. This is not an easy problem to solve because the temporal changes in both elk population size and brucellosis seroprevalence are relatively slow, requiring a long time-series in any one location to be informative. As a result, the spatial variation among regions may be more informative than the annual variation. Within Montana, elk density is associated with the seroprevalence of brucellosis (Proffitt et al., 2015). An equilibrium assumption is being made that sites have higher prevalence due to elk density; that assumption, however, does not account for how some sites may be changing over time, whereby some areas may still be of low seroprevalence because the disease was only recently introduced in that location. Due to many of these challenges, it is likely that the effects of host density on brucellosis transmission will tend to be underestimated.

At a more local scale, measuring contact rates in free-ranging wildlife populations has traditionally been difficult. Proximity loggers, however, are a recent technological advance that records the duration and time when two loggers are within a predesigned distance from one another (Prange et al., 2006). Ideally, a proximity logger would be placed on aborted fetuses to record subsequent contacts. Fetuses recovered from other management activities could be used as a proxy to record elk-fetus contact rates (Creech et al., 2012). By feeding elk across a broader area (low-density feeding), >70% reductions in elk-fetus contact rates occurred on the feedgrounds (Creech et al., 2012). No contacts were recorded with fetuses that were randomly placed away from feedgrounds (Maichak et al., 2009). Elk-elk contacts could be considered as a surrogate for elk-fetus contacts. The contact rate (within ~2m) for a given elk pair declines with increasing group size, but the individual contact rate strongly increases with elk group size, because the number of total pairs increases with group size (Cross et al., 2013b). This suggests that large elk groups may be driving much of the transmission of brucellosis within elk populations, but this pattern is hard to observe in seroprevalence data due to the frequent mixing of individuals across groups of different sizes. Therefore, additional research may consider treatments (e.g., targeted hunting, increased predator tolerance in some areas, hazing operations) that affect the group size distribution (and in particular, large groups).

Within bison, a frequency dependent model of brucellosis transmission appears to be more consistent with the available data compared to a density dependent model (Hobbs et al., 2015). During the time-series where seroprevalence data were available, the bison population size ranged from 2,000-5,000 individuals, while the seroprevalence remained relatively constant. This may be due to the grouping behavior of bison in YNP, whereby the bison group size distribution appears to be relatively constant even when the population size is dramatically reduced by boundary removals (Cross et al., 2013c). Thus, although fetus exposure rates may be higher in larger groups of bison (i.e., density dependent transmission at the group scale), more groups are created as the bison population gets larger. As a result, group sizes are relatively constant, so that disease transmission at the population scale appears frequency dependent. Therefore, the indiscriminant reduction of bison populations is unlikely to affect brucellosis transmission in bison.

4. SUPPLEMENTAL FEEDGROUNDS

The previous NRC review in 1998 highlighted the role of the supplemental feedgrounds in exacerbating brucellosis in elk. None of the research conducted since that review refutes that conclusion. The seroprevalence of disease on the feedgrounds remains high (~20%) relative to elk populations in other regions, particularly outside of the Greater Yellowstone Ecosystem (Scurlock and Edwards, 2010). As noted above, feedground sites that were fed for longer and later into the spring had higher levels of seroprevalence (Cross et al., 2007). This is probably because abortion events appear to be about five times more frequent in March, April, and May than they are in February; no abortion events have been recorded in January (Cross et al., 2015).

Supplemental feedgrounds played a role in the historic seeding of *B. abortus* infections in other, distant elk populations (Kamath et al., 2016) and in increased local elk-elk transmission (Cross et al., 2007).

Revisiting Brucellosis in the Greater Yellowstone Area

Feedgrounds, however, potentially mitigate local cattle risk compared to an area with similar elk seroprevalence without feedgrounds because they separate elk from cattle during the majority of the transmission season. From 2002-2014, only 3 of the 22 affected cattle herds were in regions with feedgrounds despite the high seroprevalence in elk during that entire time span on feedgrounds, whereas the seroprevalence in elk in other regions has only more recently increased (Brennan, 2015).

5. POTENTIAL EFFECTS OF PREDATORS AND SCAVENGERS ON BRUCELLOSIS

Wolves were reintroduced in the GYA in 1995 and were only briefly mentioned in the previous NRC report (1998). But, the potential role that wolves may have on elk or bison demography, space-use, and aggregation patterns has been an active area of research since that time. Predators may preferentially kill infected prey and may in turn reduce the level of disease (Packer et al., 2003). The mortality hazard of brucellosis-infected African buffalo (*Syncerus caffer*) is about two times higher than of uninfected individuals (95% CI = 1.1-3.7) (Gorsich et al., 2015). Predation on brucellosis-infected hosts may occur due to arthritis and lower body conditions that are associated with brucellosis infections (Gorsich et al., 2015). However, if these complications occur after the infectious period of the disease, predation is unlikely to affect the transmission dynamics. The direct effects of predation on disease dynamics are higher for diseases where infected individuals are weakened prior to and during the infectious period. For Wyoming feed-ground elk, evidence does not suggest a decreased survival rate of elk infected with brucellosis (Benavides et al., 2017). A better test of selective predation would be in areas of more intensive wolf presence, but the seroprevalence of brucellosis in YNP elk has historically been relatively low, making it difficult to study the survival rates of seropositive and seronegative elk or bison (Ferrari and Garrott, 2002; Barber-Meyer et al., 2007). Outside the borders of national parks, hunting is the dominant cause of adult elk mortality, and hunters are unlikely to be selective for infected elk. Thus, there is no current evidence to suggest that predators are selective for brucellosis-infected elk or bison.

Wolves may affect brucellosis transmission by altering population size, distribution, or aggregation patterns (see Chapter 2), which may then affect contact and disease transmission rates. The behavioral effects of wolves on elk aggregation patterns would likely occur on shorter rather than longer time frames, and they are unlikely to have longer-term population level effects of reduced survival and/or recruitment. Creel and Winnie (2005) found that the mean elk group size declined on days when wolves were present from 22 to 9. Similarly, Proffitt and colleagues (2009) found that in the presence of wolves, elk were more disaggregated in sagebrush areas. In grassland areas, however, elk were aggregated in larger average group sizes in response to increasing wolf predation risk (Gower et al., 2009; Proffitt et al., 2009). Even though the majority of elk groups are relatively small in size, the majority of elk (as individuals) tend to be in the largest groups (Hebblewhite and Pletscher, 2002; Brennan et al., 2015). In combination with increasing contact rates in the largest groups, this suggests that the majority of disease transmission may occur in large groups (Cross et al., 2013b). Thus, average elk group sizes may not be an important metric for inference about disease transmission. Wolves may shift the spatial distribution of elk either by affecting elk behavior and dispersal or altering the population growth rate of elk. While the impacts of wolves on elk calves are well documented (Wright et al., 2006), evidence is limited, which indicates that wolves have behaviorally shifted elk distributions at broad spatial scales.

Wolves appear to be attracted to large elk group sizes, as the 90th percentile of the elk group size distribution is positively correlated with wolf abundance on open and private lands (Brennan et al., 2015). Over the longer term, wolves are likely to reduce elk population sizes, although the degree of reduction that is directly attributable to wolves remains contested due to the potential confounding effects of hunting, changing climate, and other predators (Vucetich et al., 2005; Middleton et al., 2013; Christianson and Creel, 2014). An interesting correlation has been found between fecal progesterone, the number of calves per 100 adult female elk, and the ratio of wolves to elk, which suggest that wolves may reduce elk reproduction (Creel et al., 2007). While the strength of this finding has been disputed (White et al., 2011; Creel et al., 2013; Christianson and Creel, 2014; Proffitt et al., 2014), if it is true, wolves would potentially directly reduce brucellosis transmission by reducing the primary mechanism of transmission—pregnancy and the

Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

associated abortion events. Finally, in the northern range of Yellowstone the percentage of elk spending the winter outside of YNP has increased coincident with the arrival of wolves (MacNulty, 2015). Migratory elk in the Clarks Fork region of Wyoming had reduced pregnancy and calf:cow ratios relative to nonmigratory elk, which had lower exposure to wolves and bears (Middleton et al., 2013). Over time, this would result in higher populations of elk remaining on private lands throughout the year. Due to the relatively slow changes in elk populations and brucellosis seroprevalence along with many potential confounding factors, it is difficult to currently assess these short- and long-term effects of wolves on brucellosis in elk.

The previous NRC report (1998) reviewed the number of carnivores seropositive for brucellosis, presumably due to consuming infectious material. Even though Davis and colleagues (1988) demonstrated that coyotes were able to infect cattle when held in a confined space and *B. abortus* could remain viable in coyote feces and urine, carnivores are probably dead-end hosts and not likely to reinfect ungulates (NRC, 1998). To date, there has been no subsequent research that would further support or contradict that conclusion. Aune and colleagues (2012) found that half of fetuses were moved over 100m and one was moved almost 2 miles by a red fox, confirming that carnivores play a role in locally transporting infectious material to new locations (NRC, 1998). However, the 1998 NRC report suggested that “a healthy complement of predators [is] almost certain to be a major factor in reducing the probability of *B. abortus* transmission within the wildlife community and between wildlife and domestic stock. Predation and scavenging by carnivores likely biologically decontaminate the environment of infectious *B. abortus* with an efficiency unachievable in any other way.” Since 1998, several studies of fetus contact and fetus removal rates have been completed. Cook and colleagues (2004) found that the disappearance rate of bovine fetuses was, on average, 27 hrs at the NER, 40 hrs at other Wyoming feedgrounds, and 58 hrs at the Grand Teton National Park and coyotes were the dominant scavenger. Similarly, Maichak and colleagues (2009) found that 70% (28 of 40) of elk fetuses were removed within 24 hrs from the Wyoming state feedgrounds, while only 38% (3 of 8) were removed within 24 hrs from neighboring winter range locations. In contrast, fetus removal rates around YNP averaged 18 days, with a maximum of 78 days (Aune et al., 2012). Also, *B. abortus* remained viable on the underside of fetuses for a median of 30 days, but exposed areas had a median survival time of 10 days (Aune et al., 2012). Collectively, these data suggest that scavengers are removing fetuses faster from the feedgrounds than from other areas, which may be one reason why the seroprevalence in elk at the feedgrounds (20%) is roughly equivalent to the seroprevalence in some non-fed elk populations despite the more intense aggregations on the feedgrounds. Despite the potential positive role coyotes might have on scavenging to reduce brucellosis transmission, coyotes are removed by the U.S. Department of Agriculture’s Animal and Plant Health Inspection Service’s Wildlife Services at the request of landowners to reduce predation and livestock losses. In addition, coyotes are not regulated and can be shot year-round without a license in Idaho, Montana, and Wyoming. The effects these removals may have on brucellosis transmission are poorly known and require further study.

6. EFFECT OF DISEASE ON BISON AND ELK POPULATIONS

Although *B. abortus* induces abortion events and has the potential to have significant impact on individual animals (such as testicular abscesses, retained placentas, arthritis, death of neonates), it is not generally considered a direct threat to the sustainability of either elk or bison populations. Fuller and colleagues (2007) estimated that the complete eradication of brucellosis from bison would increase bison population growth rate by 29%, and similar results were found by others (Ebinger et al., 2011; Hobbs et al., 2015). This increase in population growth would most likely result in increased bison removals at the boundary. Cross and colleagues (2015) estimated that 16% (95% CI = 10, 23) of seropositive pregnant female elk will abort every year. Based on those estimates, the expectation is that an area with 30% seroprevalence would only experience a 5% decline in the population growth rate even if there were no compensatory shifts in calf mortality due to brucellosis. However, Foley and colleagues (2015) found no relationship between brucellosis seroprevalence and the ratio of elk calves to adult females at the EMU scale.

Revisiting Brucellosis in the Greater Yellowstone Area

REFERENCES

- Anderson, R.M., and R.M. May. 1991. *Infectious Diseases of Humans: Dynamics and Control*. Oxford, UK: Oxford University Press.
- Aune, K.E., J.C. Rhyhan, R. Russell, T.J. Roffe, and B. Corso. 2012. Environmental persistence of *Brucella abortus* in the Greater Yellowstone Area. *Journal of Wildlife Management* 76(2):253-261.
- Barber-Meyer, S.M., P.J. White, and L.D. Mech. 2007. Survey of selected pathogens and blood parameters of northern Yellowstone elk: Wolf sanitation effect implications. *American Midland Naturalist* 158:369-381.
- Becker, N.G., and K. Dietz. 1995. The effect of household distribution on transmission and control of highly infectious diseases. *Mathematical Biosciences* 127:207-219.
- Benavides, J.A., D. Caillaud, B.M. Scurlock, E.J. Maichak, W.H. Edwards, and P.C. Cross. 2017. Estimating loss of *Brucella abortus* antibodies from age-specific serological data in elk. *EcoHealth* 1-10.
- Brennan, A. 2015. Landscape-scale Analysis of Livestock Brucellosis. USDA's Animal and Plant Health Inspection Service.
- Brennan, A., P.C. Cross, M.D. Higgs, W.H. Edwards, B.M. Scurlock, and S. Creel. 2014. A multi-scale assessment of animal aggregation patterns to understand increasing pathogen seroprevalence. *Ecosphere* 5(10):art138.
- Brennan, A., P.C. Cross, S. Creel, and P. Stephens. 2015. Managing more than the mean: Using quantile regression to identify factors related to large elk groups. *Journal of Applied Ecology* 52(6):1656-1664.
- Cauchemez, S., A. Valleron, P. Boëlle, A. Flahault, and N.M. Ferguson. 2008. Estimating the impact of school closure on influenza transmission from sentinel data. *Nature* 452:750-754.
- Christianson, D., and S. Creel. 2014. Ecosystem scale declines in elk recruitment and population growth with wolf colonization: A before-after-control-impact approach. *PLOS ONE* 9(7).
- Conner, M.M., M.W. Miller, M.R. Ebinger, and K.P. Burnham. 2007. A meta-BACI approach for evaluating management intervention on chronic wasting disease in mule deer. *Ecological Applications* 17(1):140-153.
- Cook, W.E., E.S. Williams, and S.A. Dubay. 2004. Disappearance of bovine fetuses in northwestern Wyoming. *Wildlife Society Bulletin* 32(1):254-259.
- Creech, T., P.C. Cross, B.M. Scurlock, E.J. Maichak, J.D. Rogerson, J.C. Henningsen, and S. Creel. 2012. Effects of low-density feeding on elk-fetus contact rates on Wyoming feedgrounds. *Journal of Wildlife Management* 76(5):877-886.
- Creel, S., and J.A. Winnie. 2005. Responses of elk herd size to fine-scale spatial and temporal variation in the risk of predation by wolves. *Animal Behaviour* 69:1181-1189.
- Creel, S., D. Christianson, S. Liley, and J.A.J. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315(5814):960.
- Creel, S., J.A. Winnie, Jr., and D. Christianson. 2013. Underestimating the frequency, strength and cost of antipredator responses with data from GPS collars: An example with wolves and elk. *Ecology and Evolution* 3(16):5189-5200.
- Cross, P.C., W.H. Edwards, B.M. Scurlock, E.J. Maichak, and J.D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications* 17(4):957-964.
- Cross, P.C., J. Drew, V. Patrek, G. Pearce, M.D. Samuel, and R.J. Delahay. 2009. Wildlife population structure and parasite transmission: implications for disease management. Pp. 9-29 in *Management of Disease in Wild Mammals*. R.J. Delahay, G.C. Smith, and M.R. Hutchings, eds. Tokyo, Japan: Springer.
- Cross, P.C., E.K. Cole, A.P. Dobson, W.H. Edwards, K.L. Hamlin, G. Luikart, A.D. Middleton, B.M. Scurlock, and P.J. White. 2010a. Probable causes of increasing elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications* 20(1):278-288.
- Cross, P.C., D.M. Heisey, B.M. Scurlock, W.H. Edwards, M.R. Ebinger, and A. Brennan. 2010b. Mapping brucellosis increases relative to elk density using hierarchical Bayesian models. *PLOS ONE* 5(4):e10322.
- Cross, P.C., D. Caillaud, and D.M. Heisey. 2013a. Underestimating the effects of spatial heterogeneity due to individual movement and spatial scale: infectious disease as an example. *Landscape Ecology* 28(2):247-257.
- Cross, P.C., T.G. Creech, M.R. Ebinger, K. Manlove, K. Irvine, J. Henningsen, J. Rogerson, B.M. Scurlock, and S. Creel. 2013b. Female elk contacts are neither frequency nor density dependent. *Ecology* 94(9):2076-2086.
- Cross, P.C., E.J. Maichak, A. Brennan, B.M. Scurlock, J. Henningsen, and G. Luikart. 2013c. An ecological perspective on *Brucella abortus* in the western United States. *Revue Scientifique et Technique Office International des Epizooties* 32(1):79-87.
- Cross, P.C., E.J. Maichak, J.D. Rogerson, K.M. Irvine, J.D. Jones, D.M. Heisey, W.H. Edwards, and B.M. Scurlock. 2015. Estimating the phenology of elk brucellosis transmission with hierarchical models of cause-specific and baseline hazards. *Journal of Wildlife Management* 79(5):739-748.

Ecology and Epidemiology of Brucella abortus in the Greater Yellowstone Ecosystem

- Davis, D.S., F.C. Heck, J.D. Williams, T.R. Simpson, and L.G. Adams. 1988. Interspecific transmission of *Brucella abortus* from experimentally infected coyotes (*Canis latrans*) to parturient cattle. *Journal of Wildlife Diseases* 24(3):533-537.
- Dushoff, J., and S. Levin. 1995. The effects of population heterogeneity on disease invasion. *Mathematical Biosciences* 128(1-2):25-40.
- Ebinger, M.R., P.C. Cross, R.L. Wallen, P.J. White, and J. Treanor. 2011. Simulating sterilization, vaccination, and test-and-remove as brucellosis control measures in bison. *Ecological Applications* 21(8):2944-2959.
- Etter, R., and M.L. Drew. 2006. Brucellosis in elk of eastern Idaho. *Journal of Wildlife Diseases* 42(2):271-278.
- Ferrari, M.J., and R.A. Garrott. 2002. Bison and elk: Brucellosis seroprevalence on a shared winter range. *Journal of Wildlife Management* 66(4):1246-1254.
- Foley, A.M., P.C. Cross, D.A. Christianson, B.M. Scurlock, and S. Creel. 2015. Influences of supplemental feeding on winter elk calf:cow ratios in the southern Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 79(6):887-897.
- Fuller, J., B. Garrott, P.J. White, K.E. Aune, T.J. Roffe, and J.C. Rhyan. 2007. Reproduction and survival of Yellowstone Bison. *Journal of Wildlife Management* 71(7):2365-2372.
- Getz, W.M., and J. Pickering. 1983. Epidemic models: thresholds and population regulation. *American Naturalist* 121:892-898.
- Glass, K., and B. Barnes. 2007. How much would closing schools reduce transmission during an influenza pandemic? *Epidemiology* 18(5):623-628.
- Gorsich, E.E., V.O. Ezenwa, P.C. Cross, R.G. Bengis, and A.E. Jolles. 2015. Context-dependent survival, fecundity and predicted population-level consequences of brucellosis in African buffalo. *Journal of Animal Ecology* 84(4):999-1009.
- Gower, C.N., R.A. Garrott, P.J. White, S. Cherry, and N.G. Yoccoz. 2009. Elk group size and wolf predation: A flexible strategy when faced with variable risk. Pp. 401-422 in *The Ecology of Large Mammals in Central Yellowstone—Sixteen Years of Integrated Field Studies*. R.A. Garrott, P.J. White, and F. Watson, eds. San Diego, CA: Academic Press.
- Halloran, M.E., N.M. Ferguson, S. Eubank, I.M. Longini, D.A. Cummings, B. Lewis, S. Xu, C. Fraser, A. Vullikanti, T.C. Germann, D. Wagener, R. Beckman, K. Kadau, C. Barrett, C.A. Macken, D.S. Burke, and P. Cooley. 2008. Modeling targeted layered containment of an influenza pandemic in the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 105(12):4639-4644.
- Hebblewhite, M., and D. Pletscher. 2002. Effects of elk group size on predation by wolves. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 80(5):800-809.
- Hethcote, H.W. 1978. Immunization model for a heterogeneous population. *Theoretical Population Biology* 14(3):338-349.
- Hobbs, N.T., C. Geremia, J. Treanor, R. Wallen, P.J. White, M.B. Hooten, and J.C. Rhyan. 2015. State-space modeling to support management of brucellosis in the Yellowstone bison population. *Ecological Monographs* 85(4):525-556.
- Kamath, P.L., J.T. Foster, K.P. Drees, G. Luikart, C. Quance, N.J. Anderson, P.R. Clarke, E.K. Cole, M.L. Drew, W.H. Edwards, J.C. Rhyan, J.J. Treanor, R.L. Wallen, P.J. White, S. Robbe-Austerman, and P.C. Cross. 2016. Genomics reveals historic and contemporary transmission dynamics of a bacterial disease among wildlife and livestock. *Nature Communications* 7:11448.
- Kermack, W.O., and A.G. McKendrick. 1927. Contributions to the mathematical theory of epidemics. *Proceedings of the Royal Society of Edinburgh* 115:700-721.
- Lloyd-Smith, J.O., S.J. Schreiber, P.E. Kopp, and W.M. Getz. 2005. Superspreading and the effect of individual variation on disease emergence. *Nature* 438(7066):355-359.
- MacNulty, D. 2015. Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 1-2, 2015, Bozeman, MT.
- Maichak, E.J., B.M. Scurlock, J.D. Rogerson, L.L. Meadows, A.E. Barbknecht, W.H. Edwards, and P.C. Cross. 2009. Effects of management, behavior, and scavenging on risk of brucellosis transmission in elk of western Wyoming. *Journal of Wildlife Diseases* 45(2):398-410.
- May, R.M., and R.M. Anderson. 1984. Spatial heterogeneity and the design of immunization programs. *Mathematical Biosciences* 72(1):83-111.
- McCallum, H., N. Barlow, and J. Hone. 2001. How should pathogen transmission be modelled? *Trends in Ecology and Evolution* 16(6):295-300.
- McCorquodale, S.M., and F. Digiacomo. 1985. The role of wild North American ungulates in the epidemiology of bovine brucellosis: A review. *Journal of Wildlife Diseases* 21(4):351-357.

Revisiting Brucellosis in the Greater Yellowstone Area

- MDFWP (Montana Department of Fish, Wildlife & Parks). 2015. Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 1, 2015, Bozeman, MT.
- Middleton, A.D., M.J. Kauffman, D.E. McWhirter, M.D. Jimenez, R.C. Cook, J.G. Cook, S.E. Albeke, H. Sawyer, and P.J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16(8):1023-1030.
- Miller, R.E., J.B. Kaneene, S.D. Fitzgerald, and S.M. Schmitt. 2003. Evaluation of the influence of supplemental feeding of white-tailed deer (*Odocoileus virginianus*) on the prevalence of bovine tuberculosis in the Michigan wild deer population. *Journal of Wildlife Diseases* 39(1):84-95.
- NRC (National Research Council). 1998. *Brucellosis in the Greater Yellowstone Area*. Washington, DC: National Academy Press.
- Packer, C., R.D. Holt, P.J. Hudson, K.D. Lafferty, and A.P. Dobson. 2003. Keeping the herds healthy and alert: Implications of predator control for infectious disease. *Ecology Letters* 6:797-802.
- Prange, S., T. Jordan, C. Hunter, and S.D. Gehrt. 2006. New radiocollars for the detection of proximity among individuals. *Wildlife Society Bulletin* 34(5):1333-1344.
- Proffitt, K.M., J.L. Grigg, K.L. Hamlin, and R.A. Garrott. 2009. Contrasting effects of wolves and human hunters on elk behavioral responses to predation risk. *Journal of Wildlife Management* 73(3):345-356.
- Proffitt, K.M., J.A. Cunningham, K.L. Hamlin, and R.A. Garrott. 2014. Bottom-up and top-down influences on pregnancy rates and recruitment of northern Yellowstone elk. *Journal of Wildlife Management* 78(8):1383-1393.
- Proffitt, K.M., N. Anderson, P. Lukacs, M.M. Riordan, J.A. Gude, and J. Shamhart. 2015. Effects of elk density on elk aggregation patterns and exposure to brucellosis. *Journal of Wildlife Management* 79(3):373-383.
- Rhyan, J.C., P. Nol, C. Quance, A. Gertonson, J. Belfrage, L. Harris, K. Straka, and S. Robbe-Austerman. 2013. Transmission of brucellosis from elk to cattle and bison, Greater Yellowstone area, U.S.A., 2002-2012. *Emerging Infectious Diseases* 19(12):1992-1995.
- Rudolph, B.A., S.J. Riley, G.J. Hickling, B.J. Frawley, M.S. Garner, and S.R. Winterstein. 2006. Regulating hunter baiting for white-tailed deer in Michigan: Biological and social considerations. *Wildlife Society Bulletin* 34(2):314-321.
- Scurlock, B.M., and W.H. Edwards. 2010. Status of brucellosis in free ranging elk and bison in Wyoming. *Journal of Wildlife Diseases* 46(2):442-449.
- Treanor, J.J., C. Geremia, P.H. Crowley, J.J. Cox, P.J. White, R.L. Wallen, and D.W. Blanton. 2011. Estimating probabilities of active brucellosis infection in Yellowstone bison through quantitative serology and tissue culture. *Journal of Applied Ecology* 48(6):1324-1332.
- Vucetich, J.A., D.W. Smith, and D.R. Stahler. 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. *Oikos* 111(2):259-270.
- White, P.J., R.A. Garrott, K.L. Hamlin, R.C. Cook, J.G. Cook, and J.A. Cunningham. 2011. Body condition and pregnancy in northern Yellowstone elk: Evidence for predation risk effects? *Ecological Applications* 21(1):3-8.
- White, P.J., K.M. Proffitt, and T.O. Lemke. 2012. Changes in elk distribution and group sizes after wolf restoration. *The American Midland Naturalist* 167(1):174-187.
- Wright, G.J., R.O. Peterson, D.W. Smith, and T.O. Lemke. 2006. Selection of Northern Yellowstone Elk by Gray Wolves and Hunters. *Journal of Wildlife Management* 70(4):1070-1078.

4

Scientific Progress and New Research Tools

The scientific knowledge base of *Brucella abortus* and *B. abortus*-induced disease pathogenesis has expanded since the previous 1998 National Research Council (NRC) report was issued. This chapter provides a summary of progress since 1998 in understanding *B. abortus* infection biology; diagnosis of brucellosis in cattle, bison, and elk; and *Brucella* vaccinology. Coupled with systems biology, there is now the ability to more fully understand the infectious process of *B. abortus* and enable more rapid discovery of brucellosis vaccines and diagnostics for elk and bison.

1. INFECTION BIOLOGY AND PATHOGENESIS OF *B. ABORTUS* IN CATTLE, BISON, AND ELK

1.1 Background

When *Brucella abortus* come in contact with mucous membranes in the alimentary or respiratory tracts of the host, they invade by attaching to host epithelial cells and quickly transmigrate across the mucosa, where they are engulfed by phagocytic cells. The *Brucella*-containing phagocytic cells disseminate to regional draining lymph nodes and the blood by the lymphatic system, establishing an intermittent bacteremia. They can then colonize the placenta, fetus, mammary glands, testes, and regional draining lymph nodes of those tissues or organs; colonization of the placenta and fetus frequently results in abortion.

Brucellae primarily replicate within macrophages, neutrophils, dendritic cells, and placental trophoblasts using different survival strategies; however, the pathogen has the ability to replicate in a wide variety of additional mammalian cell types, including epithelial cells and endothelial cells. The intracellular growth and survival of *Brucella* in specialized compartments limits exposure to the host immune responses, sequesters the organism from the effects of some antibiotics, and is responsible for the unique features of pathology in infected hosts (Anderson and Cheville, 1986; Myeni et al., 2013; Celli and Tsolis, 2015; de Figueiredo et al., 2015). The pathology in pregnant ruminants is typically divided into three phases: the incubation phase, which is before clinical signs are evident; the acute phase, during which the pathogen is disseminated among host tissues; and the chronic phase, during which massive replication *B. abortus* occurs in the placental trophoblasts resulting in severe necrotizing placentitis and fetal death (Anderson and Cheville, 1986). Chronic infection results from the ability of the organism to persist in the cells of the host, which is variable for cattle, elk, and bison (Qureshi et al., 1996; Olsen, 2010).

1.2 Infection Biology and Molecular Pathogenesis

While research on the infection biology and molecular pathogenesis of brucellosis has made tremendous progress since the 1998 NRC report, several aspects of the host-*Brucella* relationship remain to be elucidated (Atluri et al., 2011). For example, it is now known how *Brucella* enter host cells (Rossetti et al., 2012) and exploit this ability to cross mucosal surfaces (Rossetti et al., 2012, 2013). However, the receptors involved in binding host cells are only partially understood (Castaneda-Roldán et al., 2004; Seabury et al., 2005). The intracellular invasion and survival of *Brucella* depends largely on its Type IV secretion system,

Revisiting Brucellosis in the Greater Yellowstone Area

although exact targets of its effectors are still elusive (O’Callaghan et al., 1999; Comerici et al., 2001; de Jong and Tsolis, 2012; Chandran, 2013; Lacerda et al., 2013; Myeni et al., 2013; Ke et al., 2015).

After entering the host, *Brucella* foils host protective responses by evading the so-called innate immune responses (Barquero-Calvo et al., 2007; Carvalho Neta et al., 2008; Gorvel, 2008; de Jong et al., 2010; Gomes et al., 2012; Rossetti et al., 2012; von Bargen et al., 2012). *Brucella* dampens inflammatory responses, relative to what occurs with other pathogens that infect through the gut mucosa (Oliveira et al., 2008; Rossetti et al., 2013). *Brucella* also restricts proinflammatory immune responses, including maturation of cells known as dendritic cells, which are crucial for induction of protective adaptive immune responses (Radhakrishnan et al., 2009; Sengupta et al., 2010; Chaudhary et al., 2012; Kaplan-Turkoz et al., 2013; Smith et al., 2013). The curtailed host immune responses together—with *Brucella*’s ability to live inside host cells and adapt to low oxygen tension—make it a successful pathogen (Kohler et al., 2002, 2003; Billard et al., 2007; Al Dahouk et al., 2008; Lamontagne et al., 2009; Barbier et al., 2011; Hanna et al., 2013). Because *Brucella* can persist inside host cells indefinitely, this contributes to its spread within the host, including to placental trophoblasts, fetal lung, male genitalia, skeletal tissues, reticuloendothelial system, and endothelium (Kim et al., 2013; Roop and Caswell, 2013; Xavier et al., 2013).

Because minimal information is available to describe the interaction of *Brucella* with target cells and tissue, a holistic systems biology analysis of the pathogenesis of brucellosis at the level of the whole host is needed for bison, elk, and cattle (Carvalho Neta et al., 2008; Delpino et al., 2009; Rossetti et al., 2013; Sankarasubramanian et al., 2016). Identification of the most critical components of pathogenesis will enhance the ability to rationally design vaccines, diagnostics, and therapeutics for elk and bison. Fortunately, many of the currently available molecular approaches and methods can be directly applied to *in vitro* and *in vivo* research on both the pathogen and the host for a comparative molecular pathogenesis approach.

1.3 Clinical Disease

Under natural conditions, a *B. abortus* infection is usually acquired by contact with the placenta, fetus, fetal fluids, or vaginal discharges from infected cows in all three host species of interest (cattle, bison, elk). Studies both before and since 1998 have shown that following infection, clinical manifestations of *B. abortus* infection in bison are largely similar to those of cattle (Nicoletti, 1980; Davis et al., 1990, 1991; Rhyan et al., 1994, 2009; Roffe, 1999a,b; Olsen and Holland, 2003; Olsen et al., 2009; Xavier et al., 2009, 2010; Van Campen and Rhyan, 2010). Since 1998, it has been confirmed that elk are also similar in that systemic clinical signs do not usually occur in the acute stages of infections (Thorne and Morton, 1978; Kreeger et al., 2000; Cook et al., 2002; Kreeger et al., 2002; Van Campen and Rhyan, 2010). In the later stages of infection, the primary clinical disease manifestations are fetal or newborn death, weak calves, metritis with retained placentas—although it is now known that the latter does not occur in elk (Rhyan et al., 2009). Abortions usually occur during the second half of gestation, accompanied by mild mastitis and reduced milk production. After the first abortion, subsequent pregnancies are generally normal, with cows occasionally giving birth to weak calves. But because *B. abortus* infection may persist, organisms can still be shed in milk and uterine discharges (Meador et al., 1989). In chronic stages of brucellosis, infertility may occur in both sexes due to metritis in cows or orchitis, epididymitis, seminal vesiculitis, and testicular abscesses in bulls, with arthritis and hygromas developing after long-term *B. abortus* infections.

1.4 Pathology and Pathogenesis

The pathogenesis of brucellosis has been most extensively studied by *in vitro* and *in vivo* experiments in nontarget hosts, especially the murine model (Cheers, 1984; Tobias et al., 1993; Grillo et al., 2000; Silva et al., 2011). While studies in models have revealed extensive valuable information on the molecular pathogenesis of brucellosis, these models do not reflect the important differences in the infection biology of brucellosis in elk, bison, and cattle (Olsen and Palmer, 2014). Studies of the molecular pathogenesis in elk, bison, and cattle have been largely limited because of onerous Select Agent requirements, lack of large

Scientific Progress and New Research Tools

animal biocontainment facilities, and costs for large animal experiments. As a consequence, few critical studies have been conducted.

The principal lesions of all three species occur in adult female and male reproductive tracts—the placenta and testes, respectively—and the fetal respiratory tract (Rhyan, 2013). The gross pathology and histopathology of infected elk, bison, and cattle have been described in varying levels of detail (Thorne and Morton, 1978; Rhyan et al., 1997, 2001; Xavier et al., 2009, 2010; Olsen and Palmer, 2014), but the pathological lesions are more similar than they are different among the three host species (Payne, 1959; Thorne and Morton, 1978; Davis et al., 1990; Samartino and Enright, 1993; Williams et al., 1993; Rhyan et al., 1994, 1997, 2001, 2009, 2010; Palmer et al., 1996; Adams, 2002; Xavier et al., 2009; Carvalho Neta et al., 2010; Poester et al., 2013; Rhyan, 2013). Nonetheless, there are some significant differences in animal behavior, disease expression, and susceptibility to brucellosis. For example, elk normally calve in solitary confined conditions in contrast to cattle and bison where parturition is a herd event that attracts other members to sniff and lick the calf or aborted fetus (Van Campen and Rhyan, 2010), potentially affecting the exposure dose of *B. abortus* and thus the transmission and frequency of disease. Studies on elk have shown they rarely have mastitis or retained placentas compared to cattle and bison, which means they may be less negatively affected by the disease (Rhyan, 2013).

Bison may be considerably more susceptible to brucellosis than cattle, as abortions occurred in <2% of pregnant cattle vaccinated with the *B. abortus* strain 19 (S19) vaccine compared to 58% of pregnant vaccinated bison (Davis et al., 1991). Higher infection and abortion rates also occurred in experimentally challenged, non-vaccinated bison compared to cattle (Olsen, 2010; Olsen and Johnson, 2011). Additionally, clearance time of the *B. abortus* RB51 vaccine is twice as long in bison as compared to cattle, yet less bacterial colonization of the udder and less mastitis is seen in bison than in cattle (Cheville et al., 1992; Roffe et al., 1999a,b; Rhyan et al., 2001).

2. DIAGNOSTICS

2.1 Background

Diagnostic assays are vital for the identification of brucellosis in humans and animals for clinical, regulatory, and research purposes (Bricker, 2002a). Bacterial and antibody detection have had key roles in the brucellosis eradication program since its inception in 1934, and there have been numerous advancements in the area of diagnostics in the past few decades.

Multiple diagnostic approaches have been used in both domestic and wild animals. Livestock surveillance initially tested all cattle within a vicinity, but it has evolved to focus on animals at surveillance nodes where cattle are accessible, such as slaughter and first point testing (e.g., markets, shows, and sales), while maintaining wide area testing in communities with known infections. Whole herd follow-up testing has also been a mainstay in surveillance, trace-back, and eradication programs. All have used serological assays in a tiered approach with initial high-sensitivity assays followed by confirmatory testing using assays with greater specificity.

Isolation of the bacteria through culture and subsequent identification of *B. abortus* has been important for confirmation (the so-called gold standard) in serologically positive animals. However, the success of culture is dependent on a number of variables. For example, in chronically infected animals, *B. abortus* may only be present in certain lymph nodes and in fewer numbers than in acutely affected animals. Thus, while a culture positive animal is confirmed as infected with brucellosis, false negative culture results can be obtained if inappropriate tissues are collected or if tissues are not properly collected and handled during collection or laboratory processing. Additionally, in an infected population, sera from animals in early stages of infection or with latent infection may not exhibit positive test reactions (O'Grady et al., 2014).

Revisiting Brucellosis in the Greater Yellowstone Area

2.2 DNA-Based Identification of *B. abortus*

Compared to clinical settings, researchers have been able to use a broader repertoire of diagnostic assays in brucellosis research. In particular, multiple DNA amplification and detection methods provide sensitive and rapid identification and quantification of *B. abortus* in tissues and fluids originating from live and dead animals. Detection of *B. abortus* by polymerase chain reaction (PCR) is useful for research purposes, where a positive PCR result after experimental infection is definitive evidence of the presence of *B. abortus*. The specificity of singleplex and quantitative PCR (qPCR) assays used in research are excellent at the genus level, although much lower at the species and subspecies levels without modification of amplification primers and conditions (Bricker, 2002b; Tiwari et al., 2014). However, neither singleplex nor qPCR are a part of routine diagnostic and regulatory program testing.

Other means of specifically identifying various *Brucella* species, strains, and biovars by DNA-based methods have been developed, including multiplex assays targeting multiple genes and genomic regions, restriction fragment length polymorphisms, and the use of tandem repeat sequences. It can be challenging to determine both analytic and diagnostic sensitivity and specificity for multiplex assays, which impacts the decision-making process for accepting these tests for regulatory purposes. Nevertheless, multiplex PCR assays—such as the “AMOS” test, the “Bruce Ladder,” and more recent modifications of these tests—can differentiate multiple *Brucella* species and biovars and can differentiate both S19 and RB51 strains from wild type *B. abortus* (Bricker et al., 2003; López-Goñi et al., 2008; Kang et al., 2011).

2.3 Serology

Obtaining tissues for culture is often infeasible in wildlife populations, and culturing *B. abortus* is not always successful from infected animals. As a result, antibody detection is used as a proxy for infection (Gilbert et al., 2013). Serological tests reveal past exposure but not necessarily whether an individual is actively infectious, and the interpretation of seropositivity relative to the likelihood of an animal being infected needs to be evaluated relative to the knowledge of the population being tested (Nielsen and Duncan, 1990). In populations where prevalence is high, results are less likely to be false positives and more likely to be accurate indicators of disease (Gilbert et al., 2013). Although some animals may become transiently seropositive yet not infected after exposure, those animals usually do not retain a positive titer for the long term.

A positive serological result is an accurate indicator of infection in bison (Clarke et al., 2014). *Brucella abortus* biovar 1 was cultured from all but 3 of 36 seropositive bison (91%), and of the 88 seronegative bison, none had positive results of culture from any tissues (Clarke et al., 2014). Furthermore, infected seropositive bison cows likely remain seropositive and infected for a prolonged time, with positive antibody titers to *B. abortus* remaining remarkably stable over time (Rhyan et al., 2009).

The ability of an infected animal to transmit brucellosis varies depending largely on the reproductive status of that animal. Therefore, predicting “infectiousness” of a particular animal in a known infected population can be difficult. For disease management purposes, all seropositive animals in a known infected population would be considered likely to be infected with the potential to be infectious to other animals at various times.

The types of serological tests and algorithms for identifying *B. abortus*-infected cattle and bison for regulatory purposes is outlined in the U.S. Department of Agriculture’s Animal and Plant Health Inspection Service’s Uniform Methods and Rules (UM&R) for brucellosis eradication, and the Standard Operating Procedures for Submission and Testing of Brucellosis Serological Specimens (USDA-APHIS, 2003, 2014). The currently accepted testing procedures for serology that are most commonly used in approved brucellosis testing laboratories include the Buffered Acidified Plate Antigen (BAPA), Rapid Automated Presumptive (RAP) Examination, Fluorescence Polarization Assay (FPA), and Complement Fixation (CF) tests. Under certain conditions, the UM&R also allows for the use of other tests, such as Card Agglutination, Particle Concentration Fluorescence Immunoassay (PCFIA), and IDEXX HerdCheck Milk Antibody ELISA, as well as the various brucellosis milk surveillance tests for herd testing.

Scientific Progress and New Research Tools

While the FPA has been much more broadly adopted over the past decade in laboratories approved for brucellosis testing, there have been no new developments for routinely used regulatory tests since the 1998 report. This largely reflects the confidence in the level of validation resulting from decades of use that is the basis for regulatory decision making. As specified in the UM&R, these assays are approved for use in both cattle and bison testing.

Cross-reactions are possible in serological assays due to antibodies directed against other bacteria (e.g., *E. coli*, *Salmonella*, *Francisella* and *Yersinia* spp.). These cross-reactions appear as false positives and affect the specificity of the diagnostic test. In general, serological tests in cattle have high specificities (>96%), suggesting that false positives are relatively rare in cattle (Nielsen, 2002). Similarly, cross-reactivity does not appear to be a problem in bison (See et al., 2012), and the BAPA, Card, SPT, RIV, and CF tests are of high specificity in elk (Clarke et al., 2015). When the seroprevalence began to increase in some elk herds in Montana, it was suspected that the cause was cross-reactions with *Y. enterocolitica* O-antigen side chain epitopes (Shumaker et al., 2010). As a result, there was an increased use of the western blot test to rule out potential cross-reactions (Gevoek, 2006; Anderson et al., 2009). However, Montana Department of Fish, Wildlife & Parks noted that three of seven culture positive elk samples for which blood samples are also available were incorrectly identified as *Yersinia* cross-reactions by the western blot test (Anderson et al., 2009). In recent unpublished work provided to the committee, researchers with the Wyoming Game & Fish Department (WGFD) have demonstrated under experimental conditions that routine tests used for *B. abortus* diagnosis in cattle and bison (such as RAP, FPA, and others) show cross-reactions using serum from *Brucella*-negative, *Yersinia enterocolitica*-infected elk. However, elk titers against *Y. enterocolitica* do not persist beyond an average of 4 months after infection (personal communication, W.H. Edwards, 2015). The lack of persistent titers, together with the relatively few false positives observed in areas without brucellosis, suggest that cross-reactivity observed with *Yersinia*-infected elk may be minimal (Clarke et al., 2015). Lastly, immunoblot testing is, in general, more difficult to perform and interpret consistently in the diagnostic laboratory, which makes quality management a challenge. For these reasons, the western blot is not the best routine assay for detecting *Brucella*-infected elk.

2.4 Elk Testing and Interpretation

The BAPA test is the best alternative among existing and commonly used *Brucella* diagnostic assays to screen elk serum for *Brucella* antibodies, as indicated by data on sensitivity and specificity of various routinely used *Brucella* antibody detection assays (CT, rivanol, standard plate, CF, and BAPA) (Clarke et al., 2015). Consistent with these data, the United States Animal Health Association passed a resolution in 2011 recommending the use of the BAPA for presumptive testing of elk. A competitive ELISA assay has also been validated for use in elk (Van Houten et al., 2003). The cELISA can differentiate S19-vaccinated from unvaccinated but infected elk, and it has a reasonable degree of overall accuracy if the purpose of testing is to determine seroprevalence in a vaccinated elk herd. However, the cELISA failed to identify approximately 10% of elk from which it was possible to culture *B. abortus*. All culture positive elk were also positive on conventional *Brucella* serology assays. Thus, the specificity obtained by using a cELISA, while helpful in differentiating vaccinated from infected animals, was offset by somewhat reduced sensitivity. This is a disadvantage for presumptive testing of individual animals when a high degree of sensitivity is essential. There is no perfect serological test for brucellosis and no single test alone is reliable; thus, the use of multiple tests increases the confidence in diagnosis (Nielsen and Duncan, 1990).

Brucella abortus S19 vaccine has been known to cause positive test results in many animals, especially those recently vaccinated. WGFD began vaccinating elk with S19 in 1985 on the Grey's River supplemental feedground and gradually expanded the program across all the other feedgrounds except one (Dell Creek). In the supplemental feedgrounds, however, very few elk are identified as vaccine strain positive at 1.5 years or older despite the vaccination of more than 90% of juveniles. In addition, if S19 was creating false positives, one would expect a large fraction of 1.5-year-old individuals to be seropositive on

Revisiting Brucellosis in the Greater Yellowstone Area

conventional serological assays. Instead it appears as though S19-induced seroprevalence gradually increases with the age of vaccination as would be expected for field exposures. Therefore, S19 does not appear to induce long-lasting serological titers on the elk feedgrounds (Maichak et al., 2017).

A recent publication describes the use of synthetic oligosaccharides representing the O-polysaccharide side chain of *Brucella* and related species in an indirect ELISA (McGiven et al., 2015). Initial validation data provide proof of principle that synthetic oligosaccharides representing the capping M-epitope of the side chain can provide excellent specificity in discriminating antibodies against various *Brucella* species as well as *Y. enterocolitica* O:9. The use of synthetic oligos also provides a ready source of antigen without the need for culture of *B. abortus*. While additional validation data are needed to examine analytical sensitivity, diagnostic sensitivity, and diagnostic specificity, the data suggest that a better serological assay for multiple species may be available in the near future.

In 2014, Idaho, Montana, and Wyoming agreed to a uniform testing and interpretation algorithm for serological testing of elk. Both RAP examination and FPA plate tests are run in parallel on each sample. The interpretation algorithm (as shown in Figure 4-1) uses a tiered approach similar to testing of cattle for regulatory purposes. However, the current elk testing and interpretation schematic is rather complex and highlights the challenges with serological testing of elk for *Brucella* infection.

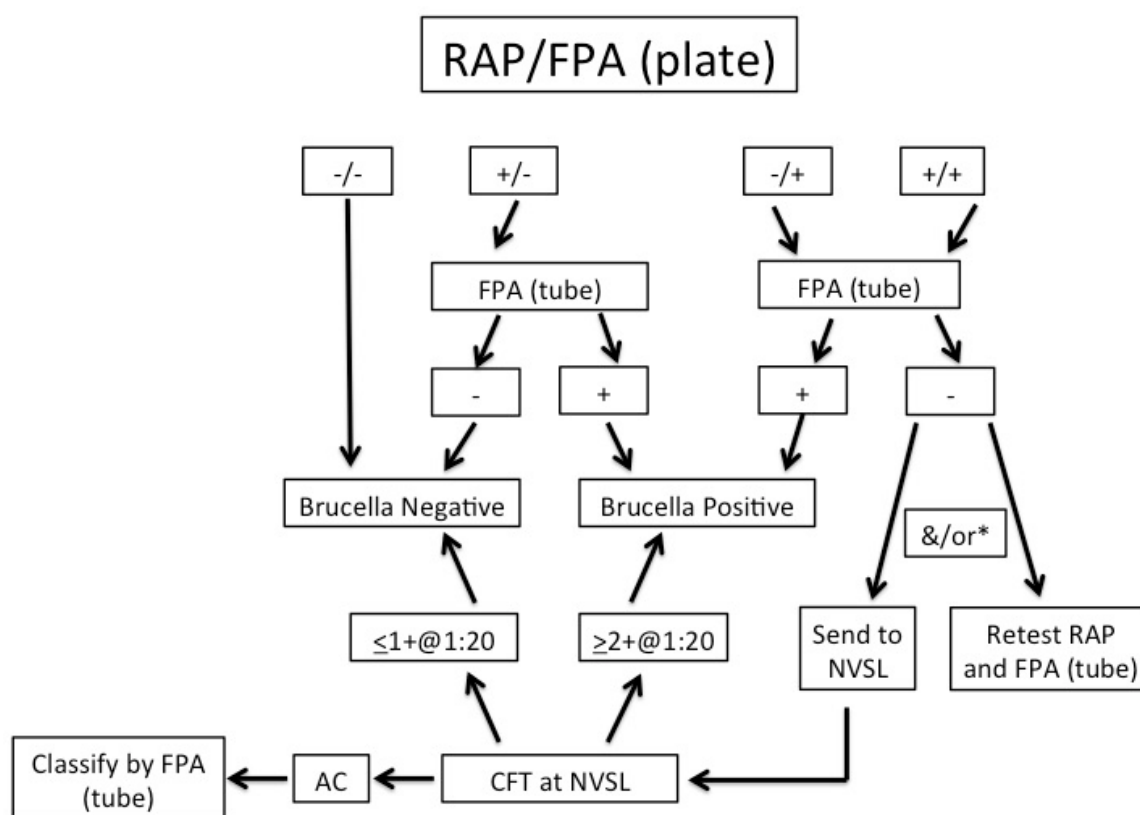


FIGURE 4-1 The Greater Yellowstone Area tristate schematic for serological testing of elk. Test abbreviations are as follows: CFT = Complement Fixation Test; FPA = Fluorescence Polarization Assay; RAP = Rapid Automated Presumptive.

NOTES: If the initial testing results are not interpretable (i.e., a “no test”), the manual card agglutination test is run.

*If initial RAP and FPA (plate) testing is positive and the FPA tube test is negative, submission to the National Veterinary Services Laboratory (NVSL) for CFT is required if the animal is outside a known brucellosis endemic area.

3. COMMERCIAL VACCINES IN WILDLIFE

B. abortus strain 19 (S19) and *B. abortus* strain RB51 (RB51) are commercially available live vaccines against *B. abortus* that are licensed for use in cattle. A number of studies to evaluate their ability to prevent infection and abortion in elk and bison are reviewed here.

3.1 Vaccination of Elk

The S19 vaccine was previously reported to be about 60% effective in preventing abortion in elk when the animals were vaccinated as calves (Thorne et al., 1981; Herriges et al., 1989). This study involved the vaccination of >40,000 elk on feedgrounds by WGFD. However, since 1998, a study found the effective rate to be much lower when a limited number of elk were evaluated in a controlled setting (Roffe et al., 2004). While there were fewer abortions in the vaccinated group relative to the unvaccinated group, the protection rate was considered too low to be efficacious, especially because *Brucella* was isolated at equal rates from the calves and fetuses in the two groups. There have been questions on whether the number of *Brucella* organisms used to infect the elk in some studies represents a dose similar to that experienced by elk at feedgrounds that come into contact with aborted fetuses (Roffe et al., 2004). In the field, the estimated exposure would be 4.1×10^6 live organisms for 10 cm diameter of skin contact (Cook, 1999). The challenge dose used in the above study was only about twice as large, making it a realistic dose, though slightly more stringent than a natural infection in the field. In another study, vaccination of feedground elk with S19 delivered via ballistics did not decrease the rate of abortion or stillbirths that occurred following infection. However, if 100% of juveniles were vaccinated, there were fewer abortion events relative to the rate that occurred when none were vaccinated (Maichak et al., 2017). Overall, S19 vaccination is considered to be inadequate for generating protective immunity in elk in the Greater Yellowstone Area.

The RB51 vaccine is composed of a mutant strain of *B. abortus* that lacks the O-polysaccharide side chain. As a result, animals vaccinated with RB51 do not make antibodies to the O-polysaccharide; the presence of such antibodies is used as an indicator of infection in conventional brucellosis diagnostic tests. Given at one of two dosages (10^9 live organisms for adults and 10^{10} for calves), RB51 is considered to be as efficacious in preventing infection and abortions in cattle as the S19 vaccine (Cheville et al., 1996; Olsen, 2000; Olsen et al., 2009). In contrast, experimental trials indicate that the RB51 vaccine is ineffective at protecting elk from brucellosis (Cook et al., 2000) in that the RB51 vaccine resulted in only low levels of protection when administered intramuscularly or by biobullets (Cook et al., 2002; Kreeger et al., 2000). Animals given a booster dose of RB51 1 year after the initial RB51 vaccination aborted at a rate equal to or higher than that of unvaccinated animals, demonstrating that RB51 is not efficacious for elk (Kreeger et al., 2002).

3.2 Immune Responses by Elk to Vaccination

Since neither S19 nor RB51 vaccines protect elk from infection or abortion, it is likely that the immune responses in elk differ from those of cattle. Immune responses are manifested as antibodies and interferon (IFN)- γ , a product of the immune system's T lymphocytes, known as a cytokine, important for controlling brucellosis. IFN- γ production can be measured using a commercially available kit made for measuring IFN- γ of red deer (Olsen et al., 2006). The expressed IFN- γ gene sequence for red deer is identical to elk except for the last amino acid; therefore, the same kit can be used to detect elk IFN- γ (Sweeney et al., 2001). Antibody responses to the vaccine strains of *B. abortus* were detected in vaccinated elk, and an expansion of CD4 T lymphocytes was seen after vaccination, but *in vitro* tests determined that lymphocyte multiplication in response to bacteria was not greater for vaccinated than for unvaccinated elk. In comparison, lymphocyte replication in response to bacteria was detected for cattle and bison cells following vaccination with RB51 (Stevens et al., 1995; Olsen et al., 2002). A similar discrepancy occurred when elk were vaccinated with *Mycobacterium bovis* (BCG), a vaccine that typically induces a strong IFN- γ response in cattle

Revisiting Brucellosis in the Greater Yellowstone Area

but not in elk, indicating that this is not peculiar to *Brucella* alone. To quantitatively and qualitatively evaluate the differences in immune responses between cattle and elk, it is necessary to first understand the elk immune system. To do this, tools are needed to identify and measure the cells and molecules involved in elk immune responses; however, those tools currently do not exist.

3.3 Vaccination of Bison

Both *B. abortus* S19 and RB51 vaccines have variable efficacy in bison (see Table 4-1). When S19 was given to adult pregnant bison—either by needle or ballistically using hollow pellets containing freeze-dried S19 organisms—50% aborted (Davis et al., 1991). This demonstrated that pregnant bison are more sensitive to abortion with S19 than pregnant cattle. Nevertheless, when bison were challenged with *B. abortus* strain 2308 (a fully virulent field isolate) in their second trimester of pregnancy, having been previously vaccinated with S19, 67% of bison were protected from abortion and 39% were protected from infection while only 4% of non-vaccinated bison failed to abort (Davis et al., 1991). These levels of protection in bison following S19 vaccination are only slightly lower than the range found for cattle. However, other studies showed that S19 vaccination of bison calves is inadequate (Davis, 1993; Davis and Elzer, 2002).

In contrast to S19, RB51 vaccination is safe in male bison, pregnant female bison, and bison calves (Elzer et al., 1998). However, a number of studies show that RB51 efficacy varies in bison adults and calves. Protection from abortion using RB51 ranged from 0% to 100%, while protection against fetal infection ranged from 0% to 81% (as summarized in Table 4-1). Calfhood vaccination of bison with RB51 was shown to provide protection from abortion when bison were challenged with virulent *B. abortus* S2308 mid-gestation in one study (Olsen et al., 2003). RB51 vaccination also reduced the recovery of S2308 from calf tissues, but not maternal tissues. In contrast, another group did not obtain significant efficacy in RB51-booster vaccinated bison (Davis and Elzer, 1999).

Studies have also shown mixed results on the efficacy of RB51 booster doses in pregnant bison. Adult pregnant bison given two doses of RB51 did not abort even though RB51 was present in fetal tissues (Olsen and Holland, 2003). Another study demonstrated that the booster dose resulted in higher IFN- γ (the immune system product associated with protective immunity to *Brucella*) responses, and none had infected fetuses (Olsen and Johnson, 2012a,b). Adult female YNP bison that had been previously vaccinated with 10^7 or 10^9 live RB51 organisms were revaccinated during the first trimester and boosted during the second trimester. An additional group of Kansas bison that had been previously vaccinated with 10^9 live RB51 organisms was also boosted during pregnancy. While abortion rates were slightly lower than for unvaccinated animals, the investigators concluded that RB51 was not significantly protective, and they questioned whether vaccination with the standard dose would be more effective (Davis and Elzer, 1999; Elzer et al., 2002). No significant differences in abortion or calf infection rates were seen among animals vaccinated once, left unvaccinated, or vaccinated twice. Thus, RB51 vaccination did not protect against abortion, and only one-third of all the calves were protected against infection in that study (Elzer et al., 2002).

To address whether booster vaccination with RB51 can enhance protection in yearlings, one group of bison heifer calves was vaccinated subcutaneously while a second group was darted (Olsen and Johnson, 2012b). All animals were naturally bred; some of the subcutaneously RB51 vaccinated animals were boosted with RB51; and pregnant bison were challenged with virulent *B. abortus* S2308. Unvaccinated controls had an 83% abortion rate compared to 33% for the animals that received a single dose of RB51, 57% for the darted animals, and none of the twice-vaccinated bison aborted. The results again indicate that multiple doses of RB51 has efficacy in bison. However, regardless of vaccination status, 100% of the fetuses/calves had viable wild type *B. abortus* in their tissues (Olsen and Johnson, 2012b).

TABLE 4-1 Summary of RB51’s Efficacy in Bison

Study	Bison Source	Vaccine Group	Bison/ Group	# of Vaccine Doses	Age of Primary and Booster Vaccinations	Vaccine Dose at 1° and Booster Vaccinations (CFUs)	Strain 2308 Challenge Dose (CFUs)*	Time of Challenge (Days of Gestation)	% Bison Protected Against Abortion	% Bison Protected Against Fetal Infection
Olsen et al., 2003	Iowa	saline	13	–	3-8 months old	0	10 ⁷	150-180	38%	38%
	Iowa	RB51	37	1	3-8 months old	1.2-6.1 × 10 ¹⁰	10 ⁷	150-180	85%	81%
Davis and Elzer, 1999	Colorado	saline	19	–	adult	0	10 ⁷	150-180	21%	Not determined
	Kansas	RB51	8	2	adult	10 ⁹ /10 ⁹	10 ⁷	150-180	50%	Not determined
	Yellowstone National Park	RB51	20	3	adult/1st trimes/ 2nd trimes.	10 ⁷ or 10 ⁹ /10 ⁹ /10 ⁹	10 ⁷	150-180	50%	Not determined
Elzer et al., 2002	South Dakota	–	27	–	6 months old	0	10 ⁷	Mid-gestation	67%	0%
	South Dakota	RB51	28	1	6 months old	10 ¹⁰	10 ⁷	Mid-gestation	75%	0%
	South Dakota	RB51	28	3	6/12/18 months old	10 ¹⁰ /10 ¹⁰ /10 ¹⁰	10 ⁷	Mid-gestation	71.4%	32%
Olsen and Johnson, 2012b	Brucellosis-free herd	saline	6	–	8-10 months old	0	10 ⁷	170-180	17%	0%
	Brucellosis-free herd	RB51	7	1	8-10 months old	darted with 1.8 × 10 ¹⁰	10 ⁷	170-180	43%	0%
	Brucellosis-free herd	RB51	6	1	8-10 months old	2.2 × 10 ¹⁰	10 ⁷	170-180	67%	0%
	Brucellosis-free herd	RB51	5	2	8-10/23-25 months old	1.1 × 10 ¹⁰ /2.2 × 10 ¹⁰	10 ⁷	170-180	100%	0%
Olsen et al., 2015	Brucellosis-free herd	saline	6	–	8-11 months old	0	10 ⁷	170-180	0%	17%
	Brucellosis-free herd	RB51	5	1	8-11 months old	1.6 × 10 ¹⁰	10 ⁷	170-180	80%	40%
	Brucellosis-free herd	RB51	14	2	8-11/19-22 months old	1.6 × 10 ¹⁰ /2.8 × 10 ¹⁰	10 ⁷	170-180	93%	57%
Olsen et al., 2009	Brucellosis-free herd	saline	8	–	10 months old	0	10 ⁷	170-180	0	0%
	Brucellosis-free herd	RB51 + <i>sodC</i> , <i>wboA</i>	6	1	10 months old	7.4 × 10 ¹⁰	10 ⁷	170-180	33%	0%
	Brucellosis-free herd	RB51	6	1	10 months old	4.26 × 10 ¹⁰	10 ⁷	170-180	66%	0%

NOTE: *Bison were challenged via the conjunctival route with virulent wild type *B. abortus* strain 2308.

Revisiting Brucellosis in the Greater Yellowstone Area

Alternative methods for delivering RB51 have been evaluated. Vaccinating bison by darts induced immune responses similar to those achieved by hand vaccination, but neither the dart nor the hand vaccination method protected the bison from abortion when challenged with *B. abortus* S2308 (Olsen and Johnson, 2012b). However, bison that were given a booster dose showed protection from abortion. A follow-up study demonstrated that giving a booster dose of RB51 results in a greater IFN- γ response as measured by mRNA transcripts, reduced percentage of abortions, and less bacterial colonization of tissues (Olsen et al., 2015).

4. NEW SCIENTIFIC TOOLS INFORMING BRUCELLOSIS INFECTION BIOLOGY, PATHOGENESIS, AND VACCINOLOGY

New molecular tools have recently been developed that link cell biology with genetics and genomics. Bioinformatics has also emerged as an important tool to manage and analyze massive datasets of biological information. The expansion of the “-omics” (fields of study related to the genome, transcriptome, proteome, metabolome), genomics tools, and next-generation sequencing technologies now enable in-depth analyses needed to understand cellular function and behavior of *B. abortus* and its hosts (including elk, bison, and cattle).

4.1 *Brucella* Genome

More than 30 complete *Brucella* genomes have been sequenced since 1998, providing a database for comparative analysis of gene structure and homologies, gene expression, regulatory networks, protein synthesis, and metabolic pathways. Gene variations among strains have been identified by comparative genomics and through speciation. The identified variations only partially explain the differences in virulence among *Brucella* species and their specificity for certain host species (He, 2012).

Genes of a pathogen can be interrogated by a process known as reverse vaccinology to identify their potential to induce immune responses in their host, and this has been applied to the *Brucella* genomes (He and Xiang, 2010; He, 2012; Gomez et al., 2013a,b; Vishnu et al., 2015). Candidate gene products have been tested for in vivo efficacy, an approach that could be used to tailor brucellosis vaccines for elk, bison, and cattle (Ko and Splitter, 2003; Wang et al., 2012; Gomez et al., 2013a,b). For example, Vaxign (a Web-based vaccinology tool) identified 14 outer membrane proteins that are conserved in six virulent strains of *B. abortus*, *B. melitensis*, and *B. suis* (He and Xiang, 2010). Some of these proteins were shown to induce antibody and T cell responses in immunized mice (Gomez et al., 2013a,b). This type of information may also be useful for developing new diagnostic tests.

Whole genome sequencing and other sequence-based technologies can show evolutionary relationships of *Brucella* relative to geography and host origin. This is a particularly relevant tool for understanding the epidemiology of *Brucella* infections among cattle, elk, and bison in Yellowstone National Park (Beja-Pereira et al., 2009; Higgins et al., 2012; Rhyan et al., 2013; Kamath et al., 2016).

Gene expression analysis of *Brucella* during host adaptation has identified critical factors for virulence and long-term survival of *Brucella* (Kim et al., 2013, 2014). Inactivation or knockout of *Brucella* genes allows gene function to be identified in pathogenesis and virulence. This could also facilitate enhanced vaccine development by producing new attenuated strains of the bacteria (O’Callaghan et al., 1999; Rosinha et al., 2002; Ficht, 2003; Arenas-Gamboa et al., 2008, 2009; Kim et al., 2014).

4.2 Host Genomes

Substantial progress has been made on assembling the *Bison bison bison* reference genome (NIH, 2016). A bison reference genome provides fundamental information and can eventually help identify any genetic basis for increased susceptibility of bison to *B. abortus*. A deer reference genome (red deer, Canadian elk) is also being completed and validated (Brauning et al., 2015). Functional genomics can detect

Scientific Progress and New Research Tools

host genes that are either expressed or repressed and could further reveal the mechanism by which *B. abortus* survives. For example, gene silencing (using RNA interference) was used to knock down specific host genes during *Brucella* infection in model systems, which allowed scientists to identify the genes controlling major infection pathways (Qin et al., 2008; Rossetti et al., 2012). While genetic resistance against brucellosis is a complex polygenic trait in cattle and bison, newer genetic tools can provide the means to better understand the genetic basis for susceptibility to *B. abortus* in elk and bison and to clone livestock or wildlife for enhanced genetic resistance to *B. abortus* (Adams and Templeton, 1998; Westhusin et al., 2007; Adams and Schutta, 2010).

Brucella and host gene expression and proteome datasets have been generated in the past decade, which will provide future opportunities for a comprehensive analysis of both host and pathogen responses during infection (Rajashekara et al., 2006; Carvalho Neta et al., 2008; Lamontagne et al., 2009; He et al., 2010; Rossetti et al., 2010, 2012, 2013; Viadas et al., 2010; Weeks et al., 2010; Lin et al., 2011; Wang et al., 2011; Liu et al., 2012; Karadeniz et al., 2015). To date, datasets have been analyzed to understand gene regulatory networks, characterize *Brucella* stress responses, and understand modulation of host responses (He et al., 2010; He, 2012; Hanna et al., 2013; Kim et al., 2013, 2014; Karadeniz et al., 2015).

5. CONCLUSION

Even though there is now a greater scientific understanding of *B. abortus* than in 1998, there continue to be major gaps in understanding infection biology and molecular pathogenesis of brucellosis in each host. New tools and reagents are needed to gain a basic understanding of the uniqueness of the elk immune system response to *Brucella* to develop elk specific vaccines. There has been limited progress in understanding *Brucella* host preference and genetic resistance to brucellosis to manage transmission between domestic animals and wildlife species (Godfroid et al., 2011, 2014), but new molecular and bioinformatics tools offer greater hope to understand these phenomena (see Chapter 9 on Remaining Gaps for Understanding and Controlling Brucellosis).

REFERENCES

- Adams, L.G. 2002. The pathology of brucellosis reflects the outcome of the battle between the host genome and the *Brucella* genome. *Veterinary Microbiology* 90(1-4):553-561.
- Adams, L.G., and C.J. Schutta. 2010. Natural disease resistance to brucellosis: A review. *The Open Journal of Veterinary Science* 4:61-71.
- Adams, L.G., and J.W. Templeton. 1998. Genetic resistance to bacterial diseases of animals. *Revue Scientifique et Technique Office International des Epizooties* 17(1):200-219.
- Al Dahouk, S., V. Jubier-Maurin, H.C. Scholz, H. Tomaso, W. Karges, H. Neubauer, and S. Kohler. 2008. Quantitative analysis of the intramacrophagic *Brucella suis* proteome reveals metabolic adaptation to late stage of cellular infection. *Proteomics* 8(18):3862-3870.
- Anderson, N.J., J.M. Ramsey, and K.D. Hughes. 2009. 2008 Brucellosis Survey Final Report. Montana Fish, Wildlife & Parks, Wildlife Laboratory, Bozeman, MT.
- Anderson, T.D., and N.F. Cheville. 1986. Ultrastructural Morphometric Analysis of *Brucella abortus*-Infected Trophoblasts in Experimental Placentitis. *American Journal of Pathology* 124(2):226-237.
- Arenas-Gamboa, A.M., T.A. Ficht, M.M. Kahl-McDonagh, and A.C. Rice-Ficht. 2008. Immunization with a single dose of a microencapsulated *Brucella melitensis* mutant enhances protection against wild-type challenge. *Infection and Immunology* 76(6):2448-2455.
- Arenas-Gamboa, A.M., T.A. Ficht, M.M. Kahl-McDonagh, G. Gomez, and A.C. Rice-Ficht. 2009. The *Brucella abortus* S19 DeltavjbR live vaccine candidate is safer than S19 and confers protection against wild-type challenge in BALB/c mice when delivered in a sustained-release vehicle. *Infection and Immunology* 77(2):877-884.
- Atluri, V.L., M.N. Xavier, M.F. de Jong, A.B. den Hartigh, and R.M. Tsolis. 2011. Interactions of the human pathogenic *Brucella* species with their hosts. *Annual Reviews in Microbiology* 65:523-541.
- Barbier, T., C. Nicolas, and J.J. Letesson. 2011. *Brucella* adaptation and survival at the crossroad of metabolism and virulence. *FEBS Letters* 585(19):2929-2934.

Revisiting Brucellosis in the Greater Yellowstone Area

- Barquero-Calvo, E., E. Chaves-Olarte, D.S. Weiss, C. Guzmán-Verri, C. Chacon-Diaz, A. Rucavado, I. Moriyón, and E. Moreno. 2007. *Brucella abortus* uses a stealthy strategy to avoid activation of the innate immune system during the onset of infection. *PLOS ONE* 2(7):e631.
- Beja-Pereira, A., B. Bricker, S. Chen, C. Almendra, P.J. White, and G. Luikart. 2009. DNA genotyping suggests that recent brucellosis outbreaks in the Greater Yellowstone area originated from elk. *Journal of Wildlife Diseases* 45(4):1174-1177.
- Billard, E., J. Dornand, and A. Gross. 2007. *Brucella suis* prevents human dendritic cell maturation and antigen presentation through regulation of tumor necrosis factor alpha secretion. *Infection and Immunology* 75(10):4980-4989.
- Brauning, R., P.J. Fisher, A.F. McCulloch, R.J. Smithies, J.F. Ward, M.J. Bixley, C.T. Lawley, S.J. Rowe, and J.C. McEwan. 2015. Utilization of high throughput genome sequencing technology for large scale single nucleotide polymorphism discovery in red deer and Canadian elk. *Proceedings of the Cold Spring Harbor Laboratory*.
- Bricker, B.J. 2002a. Diagnostic strategies used for the identification of *Brucella*. *Veterinary Microbiology* 90(1-4):433-434.
- Bricker, B.J. 2002b. PCR as a diagnostic tool for brucellosis. *Veterinary Microbiology* 90(1-4):435-446.
- Bricker, B.J., D.R. Ewalt, S.C. Olsen, and E.E. Jensen. 2003. Evaluation of the *Brucella abortus* species-specific polymerase chain reaction assay, an improved version of the *Brucella* AMOS-polymerase chain reaction assay for cattle. *Journal of Veterinary Diagnostic Investigation* 15:374-378.
- Carvalho Neta, A.V., A.P. Stynen, T.A. Paixao, K.L. Miranda, F.L. Silva, C.M. Roux, R.M. Tsolis, R.E. Everts, H.A. Lewin, L.G. Adams, A.F. Carvalho, A.P. Lage, and R.L. Santos. 2008. Modulation of the bovine trophoblastic innate immune response by *Brucella abortus*. *Infection and Immunology* 76(5):1897-1907.
- Carvalho Neta, A.V., J.P. Mol, M.N. Xavier, T.A. Paixao, A.P. Lage, and R.L. Santos. 2010. Pathogenesis of bovine brucellosis. *Veterinary Journal* 184(2):146-155.
- Castaneda-Roldán, E.I., F. Avelino-Flores, M. Dall'Agnol, E. Freer, L. Cedillo, J. Dornand, and J.A. Girón. 2004. Adherence of *Brucella* to human epithelial cells and macrophages is mediated by sialic acid residues. *Cellular Microbiology* 6(5):435-445.
- Celli, J., and R.M. Tsolis. 2015. Bacteria, the endoplasmic reticulum and the unfolded protein response: friends or foes. *Nature Reviews Microbiology* 13:71-82.
- Chandran, V. 2013. Type IV secretion machinery: Molecular architecture and function. *Biochemical Society Transactions* 41(1):17-28.
- Chaudhary, A., K. Ganguly, S. Cabantous, G.S. Waldo, S.N. Micheva-Viteva, K. Nag, W.S. Hlavacek, and C.S. Tung. 2012. The *Brucella* TIR-like protein TcpB interacts with the death domain of MyD88. *Biochemical and Biophysical Research Communications* 417(1):299-304.
- Cheers, C. 1984. Pathogenesis and cellular immunity in experimental murine brucellosis. *Development in Biological Standardization* 56:237-246.
- Cheville, N.F., A.E. Jensen, S.M. Halling, F.M. Tatum, D.C. Morfitt, S.G. Hennager, W.M. Frerichs, and G. Schurig. 1992. Bacterial survival, lymph node changes, and immunologic responses of cattle vaccinated with standard and mutant strains of *Brucella abortus*. *American Journal of Veterinary Research* 53(10):1881-1888.
- Cheville, N.F., S.C. Olsen, A.E. Jensen, M.G. Stevens, M.V. Palmer, and A.M. Florance. 1996. Effects of age at vaccination on efficacy of *Brucella abortus* strain RB51 to protect cattle against brucellosis. *American Journal of Veterinary Research* 57(8):1153-1156.
- Clarke, P.R., R.K. Frey, J.C. Rhyen, M.P. McCollum, P. Nol, and K. Aune. 2014. Feasibility of quarantine procedures for bison (*Bison bison*) calves from Yellowstone National Park for conservation of brucellosis-free bison. *Journal of American Veterinary Medical Association* 244(5):588-591.
- Clarke, P.R., W.H. Edwards, S.G. Hennager, J.F. Block, A.M. Yates, E. Ebel, D.J. Knopp, A. Fuentes-Sanchez, J. Jennings-Gaines, R.L. Kientz, and M. Simunich. 2015. Comparison of buffered, acidified plate antigen to standard serologic tests for the detection of serum antibodies to *Brucella abortus* in elk (*Cervus canadensis*). *Journal of Wildlife Diseases* 51(3):764-768.
- Comerci, D.J., M.J. Martinez-Lorenzo, R. Sieira, J.P. Gorvel, and R.A. Ugalde. 2001. Essential role of the VirB machinery in the maturation of the *Brucella abortus*-containing vacuole. *Cellular Microbiology* 3(3):159-168.
- Cook, W.E. 1999. Brucellosis in Elk: Studies of Epizootiology and Control. Ph.D. dissertation, University of Wyoming, Laramie, WY.
- Cook, W.E., E.S. Williams, E.T. Thorne, T.J. Kreeger, G.W. Stout, G. Schurig, L.A. Colby, F. Enright, and P.H. Elzer. 2000. Safety of *Brucella abortus* strain RB51 in bull elk. *Journal of Wildlife Diseases* 36(3):484-488.
- Cook, W.E., E.S. Williams, E.T. Thorne, T.J. Kreeger, G. Stout, K. Bardsley, H. Edwards, G. Schurig, L.A. Colby, F. Enright, and P.H. Elzer. 2002. *Brucella abortus* strain RB51 vaccination in elk. I. Efficacy of reduced dosage. *Journal of Wildlife Diseases* 38(1):18-26.

Scientific Progress and New Research Tools

- Davis, D.S. 1993. Summary of bison/brucellosis research conducted at Texas A & M University 1985-93. Pp. 347-361 in Proceedings of North American Public Bison Herds Symposium. H.E. Walker, ed. Denver, CO: National Bison Association.
- Davis, D.S., and P.H. Elzer. 1999. Safety and efficacy of *Brucella abortus* RB51 vaccine in adult American bison (*Bison bison*). Proceedings of the U.S. Animal Health Association 103:154-158.
- Davis, D.S., and P.H. Elzer. 2002. Brucella vaccines in wildlife. Veterinary Microbiology 90(1-4):533-544.
- Davis, D.S., J.W. Templeton, T.A. Ficht, J.D. Williams, J.D. Kopeck, and L.G. Adams. 1990. *Brucella abortus* in captive bison. I. Serology, bacteriology, pathogenesis, and transmission to cattle. Journal of Wildlife Diseases 26(3):360-371.
- Davis, D.S., J.W. Templeton, T.A. Ficht, J.D. Huber, R.D. Angus, and L.G. Adams. 1991. *Brucella abortus* in bison. II. Evaluation of strain 19 vaccination of pregnant cows. Journal of Wildlife Diseases 27(2):258-264.
- de Figueiredo, P., T.A. Ficht, A. Rice-Ficht, C.A. Rossetti, and L.G. Adams. 2015. Pathogenesis and Immunobiology of Brucellosis: Review of *Brucella*-Host Interactions. American Journal of Pathology 185:1505-1517.
- de Jong, M.F., and R.M. Tsolis. 2012. Brucellosis and type IV secretion. Future Microbiology 7(1):47-58.
- de Jong, M.F., H.G. Rolan, and R.M. Tsolis. 2010. Innate immune encounters of the (Type) 4th kind: *Brucella*. Cellular Microbiology 12(9):1195-1202.
- Delpino, M.V., C.A. Fossati, and P.C. Baldi. 2009. Proinflammatory response of human osteoblastic cell lines and osteoblast-monocyte interaction upon infection with *Brucella* spp. Infection and Immunology 77(3):984-995.
- Elzer, P.H., M.D. Edmonds, S.D. Hagius, J.V. Walker, M.J. Gilsdorf, and D.S. Davis. 1998. Safety of *Brucella abortus* strain RB51 in bison. Journal of Wildlife Diseases 34(4):825-829.
- Elzer, P., S. Hagius, T.J. Roffe, S. Holland, and D.S. Davis. 2002. Failure of RB51 calfhood bison vaccine against brucellosis. Proceedings of U.S. Animal Health Association 106:87-91.
- Ficht, T.A. 2003. Intracellular survival of *Brucella*: Defining the link with persistence. Veterinary Microbiology 92(3):213-223.
- Gevoek, N. 2006. Brucellosis tests show no spike in Madison elk. Montana Standard, April 27, 2006.
- Gilbert, A.T., A.R. Fooks, D.T.S. Hayman, D.L. Horton, T. Müller, R. Plowright, A.J. Peel, R. Bowen, J.L.N. Wood, J. Mills, A.A. Cunningham, and C.E. Rupprecht. 2013. Deciphering serology to understand the ecology of infectious diseases in wildlife. EcoHealth 10(3):298-313.
- Godfroid, J., H.C. Scholz, T. Barbier, C. Nicolas, P. Wattiau, D. Fretin, A.M. Whatmore, A. Cloeckaert, J.M. Blasco, I. Moriyon, C. Saegerman, J.B. Muma, S. Al Dahouk, H. Neubauer, and J.J. Letesson. 2011. Brucellosis at the animal/ecosystem/human interface at the beginning of the 21st century. Preventive Veterinary Medicine 102(2):118-131.
- Godfroid, J., X. DeBolle, R.M. Roop, D. O'Callaghan, R.M. Tsolis, C. Baldwin, R.L. Santos, J. McGiven, S. Olsen, I.H. Nymo, A. Larsen, S. Al Dahouk, and J.J. Letesson. 2014. The quest for a true One Health perspective of brucellosis. Revue Scientifique et Technique Office International des Epizooties 33(2):521-538.
- Gomes, M.T., P.C. Campos, L.A. de Almeida, F.S. Oliveira, M.M. Costa, F.M. Marim, G.S. Pereira, and S.C. Oliveira. 2012. The role of innate immune signals in immunity to *Brucella abortus*. Frontiers in Cellular and Infection Microbiology 2:130.
- Gomez, G., L.G. Adams, A. Rice-Ficht, and T.A. Ficht. 2013a. Host-*Brucella* interactions and the *Brucella* genome as tools for subunit antigen discovery and immunization against brucellosis. Frontiers in Cellular and Infection Microbiology 3:17.
- Gomez, G., J. Pei, W. Mwangi, L.G. Adams, A. Rice-Ficht, and T.A. Ficht. 2013b. Immunogenic and invasive properties of *Brucella melitensis* 16M outer membrane protein vaccine candidates identified via a reverse vaccinology approach. PLOS ONE 8(3):e59751.
- Gorvel, J.P. 2008. *Brucella*: A Mr. "Hide" converted into Dr. Jekyll. Microbes and Infection 10(9):1010-1013.
- Grillo, M.J., N. Bosseray, and J.M. Blasco. 2000. In vitro markers and biological activity in mice of seed lot strains and commercial *Brucella melitensis* Rev 1 and *Brucella abortus* B19 vaccines. Biologicals 28(2):119-127.
- Hanna, N., S. Ouahrani-Bettache, K.L. Drake, L.G. Adams, S. Kohler, and A. Occhialini. 2013. Global Rsh-dependent transcription profile of *Brucella suis* during stringent response unravels adaptation to nutrient starvation and cross-talk with other stress responses. BMC Genomics 14:459.
- He, Y. 2012. Analyses of *Brucella* pathogenesis, host immunity, and vaccine targets using systems biology and bioinformatics. Frontiers in Cellular and Infection Microbiology 2:2.
- He, Y., and Z. Xiang. 2010. Bioinformatics analysis of *Brucella* vaccines and vaccine targets using VIOLIN. Immunome Research 6(Suppl. 1):S5.
- He, Y., S. Sun, H. Sha, Z. Liu, L. Yang, Z. Xue, H. Chen, and L. Qi. 2010. Emerging roles for XBP1, a sUPeR transcription factor. Gene Expression 15(1):13-25.

Revisiting Brucellosis in the Greater Yellowstone Area

- Herriges, J.D., E.T. Thime, S.L. Anderson, and H.A. Dawson. 1989. Vaccination of elk in Wyoming with reduced dose strain 19 *Brucella*: Controlled studies and ballistic implant field trials. *Proceedings of the U.S. Animal Health Association* 93:640-655.
- Higgins, J., T. Stuber, C. Quance, W.H. Edwards, R.V. Tiller, T. Linfield, J. Rhyne, A. Berte, and B. Harris. 2012. Molecular epidemiology of *Brucella abortus* isolates from cattle, elk, and bison in the United States, 1998 to 2011. *Applied and Environmental Microbiology* 78(10):3674-3684.
- Kamath, P., P.C. Cross, and J.T. Foster. 2016. Genomics reveals historic and contemporary transmission dynamics of a bacterial disease among wildlife and livestock. *Nature Communications* 7:11448.
- Kang, S.I., M. Her, J.W. Kim, J.Y. Kim, K.Y. Ko, Y.M. Ha, and S.C. Jung. 2011. Advanced multiplex PCR assay for differentiation of *Brucella* species. *Applied and Environmental Microbiology* 77(18):6726-6728.
- Kaplan-Turkoz, B., T. Koelblen, C. Felix, M.P. Candusso, D. O'Callaghan, A.C. Vergunst, and L. Terradot. 2013. Structure of the Toll/interleukin 1 receptor (TIR) domain of the immunosuppressive *Brucella* effector BtpA/Btp1/TcpB. *FEBS Letters* 587(21):3412-3416.
- Karadeniz, I., J. Hur, Y. He, and A. Ozgur. 2015. Literature mining and ontology based analysis of Host-*Brucella* Gene-Gene Interaction Network. *Frontiers in Microbiology* 6:1386.
- Ke, Y., Y. Wang, W. Li, and Z. Chen. 2015. Type IV secretion system of *Brucella* spp. and its effectors. *Frontiers in Cellular and Infection Microbiology* 5:72.
- Kohler, S., V. Foulongne, S. Ouahrani-Bettache, G. Bourg, J. Teyssier, M. Ramuz, and J.P. Liautard. 2002. The analysis of the intramacrophagic virulome of *Brucella suis* deciphers the environment encountered by the pathogen inside the macrophage host cell. *Proceedings of the National Academy of Sciences of the United States of America* 99(24):15711-15716.
- Kohler, S., S. Michaux-Charachon, F. Porte, M. Ramuz, and J.P. Liautard. 2003. What is the nature of the replicative niche of a stealthy bug named *Brucella*? *Trends in Microbiology* 11(5):215-219.
- Kreeger, T.J., M.W. Miller, M.A. Wild, P.H. Elzer, and S.C. Olsen. 2000. Safety and efficacy of *Brucella abortus* strain RB51 vaccine in captive pregnant elk. *Journal of Wildlife Diseases* 36(3):477-483.
- Kreeger, T.J., W.E. Cook, W.H. Edwards, P.H. Elzer, and S.C. Olsen. 2002. *Brucella abortus* strain RB51 vaccination in elk. II. Failure of high dosage to prevent abortion. *Journal of Wildlife Diseases* 38(1):27-31.
- Kim, H.S., C.C. Caswell, R. Foreman, R.M. Roop, II, and S. Crosson. 2013. The *Brucella abortus* general stress response system regulates chronic mammalian infection and is controlled by phosphorylation and proteolysis. *Journal of Biological Chemistry* 288(19):13906-13916.
- Kim, H.S., J.W. Willett, N. Jain-Gupta, A. Fiebig, and S. Crosson. 2014. The *Brucella abortus* virulence regulator, LovhK, is a sensor kinase in the general stress responses signalling pathway. *Molecular Microbiology* 94(4):913-925.
- Ko, J., and G.A. Splitter. 2003. Molecular host-pathogen interaction in brucellosis: Current understanding and future approaches to vaccine development for mice and humans. *Clinical Microbiology Reviews* 16(1):65-78.
- Lacerda, T.L., S.P. Salcedo, and J.P. Gorvel. 2013. *Brucella* T4SS: The VIP pass inside host cells. *Current Opinion in Microbiology* 16(1):45-51.
- Lamontagne, J., A. Forest, E. Marazzo, F. Denis, H. Butler, J.F. Michaud, L. Boucher, I. Pedro, A. Villeneuve, D. Sitnikov, K. Trudel, N. Nassif, D. Boudjelti, F. Tomaki, E. Chaves-Olarte, C. Guzman-Verri, S. Brunet, A. Cote-Martin, J. Hunter, E. Moreno, and E. Paramithiotis. 2009. Intracellular adaptation of *Brucella abortus*. *Journal of Proteome Research* 8(3):1594-1609.
- Lin, Y., Z. Xiang, and Y. He. 2011. Brucellosis Ontology (IDOBUR) as an extension of the Infectious Disease Ontology. *Journal of Biomedical Semantics* 2(1):9.
- Liu, Q., W. Han, C. Sun, L. Zhou, L. Ma, L. Lei, S. Yan, S. Liu, C. Du, and X. Feng. 2012. Deep sequencing-based expression transcriptional profiling changes during *Brucella* infection. *Microbial Pathogenesis* 52(5):267-277.
- López-Goñi, I., D. García-Yoldi, C.M. Marín, M.J. de Miguel, P.M. Muñoz, J.M. Blasco, I. Jacques, M. Grayon, A. Cloeckert, A.C. Ferreira, R. Cardoso, M.I. Corrêa de Sá, K. Walravens, D. Albert, and B. Garin-Bastuji. 2008. Evaluation of a multiplex PCR assay (Bruce-ladder) for molecular typing of all *Brucella* species, including the vaccine strains. *Journal of Clinical Microbiology* 46(10):3484-3487.
- Maichak, E.J., B.M. Scurlock, P.C. Cross, J.D. Rogerson, W.H. Edwards, B. Wise, S.G. Smith, and T.J. Kreeger. 2017. Assessment of a strain 19 brucellosis vaccination program in elk. *Wildlife Society Bulletin* 41:70-79.
- McGiven, J., L. Howells, L. Duncombe, J. Stack, N.V. Ganesh, J. Guiard, and D.R. Bundle. 2015. Improved serodiagnosis of bovine brucellosis by novel synthetic oligosaccharide antigens representing the capping m epitope elements of *Brucella* O-polysaccharide. *Journal of Clinical Microbiology* 53(4):1204-1210.
- Meador, V., B. Deyoe, and N. Cheville. 1989. Effect of nursing on *Brucella abortus* infection of mammary glands of goats. *Veterinary Pathology* 26:369-375.

Scientific Progress and New Research Tools

- Myeni, S., R. Child, T.W. Ng, J.J. Kupko, III, T.D. Wehrly, S.F. Porcella, L.A. Knodler, and J. Celli. 2013. *Brucella* modulates secretory trafficking via multiple type IV secretion effector proteins. *PLOS Pathogens* 9(8):e1003556.
- Nicoletti, P. 1980. The epidemiology of bovine brucellosis. *Advances in Veterinary Science and Comparative Medicine* 24:69-98.
- Nielsen, K. 2002. Diagnosis of brucellosis by serology. *Veterinary Microbiology* 90(1-4):447-459.
- Nielsen, K., and J.R. Duncan, eds. 1990. *Animal Brucellosis*. Boca Raton, FL: CRC Press.
- NIH (National Institutes of Health). 2016. Bison bison bison (American bison) Reference Genome. Available online at https://www.ncbi.nlm.nih.gov/assembly/GCF_000754665.1 (accessed December 21, 2016).
- O'Callaghan, D., C. Cazeville, A. Allardet-Servent, M.L. Boschioli, G. Bourg, V. Foulongne, P. Frutos, Y. Kulakov, and M. Ramuz. 1999. A homologue of the *Agrobacterium tumefaciens* VirB and *Bordetella pertussis* Ptl type IV secretion systems is essential for intracellular survival of *Brucella suis*. *Molecular Microbiology* 33(6):1210-1220.
- O'Grady, D., W. Byrne, P. Kelleher, H. O'Callaghan, K. Kenny, T. Heneghan, S. Power, J. Egan, and F. Ryan. 2014. A comparative assessment of culture and serology in the diagnosis of brucellosis in dairy cattle. *The Veterinary Journal* 199(3):370-375.
- Oliveira, S.C., F.S. de Oliveira, G.C. Macedo, L.A. de Almeida, and N.B. Carvalho. 2008. The role of innate immune receptors in the control of *Brucella abortus* infection: Toll-like receptors and beyond. *Microbes and Infection* 10(9):1005-1009.
- Olsen, S.C. 2000. Responses of adult cattle to vaccination with a reduced dose of *Brucella abortus* strain RB51. *Research in Veterinary Science* 69(2):135-140.
- Olsen, S.C. 2010. Brucellosis in the United States: Role and significance of wildlife reservoirs. *Vaccine* 28(Suppl. 5):F73-F76.
- Olsen, S.C., and S.D. Holland. 2003. Safety of revaccination of pregnant bison with *Brucella abortus* strain RB51. *Journal of Wildlife Diseases* 39(4):824-829.
- Olsen, S.C., and C. Johnson. 2011. Comparison of abortion and infection after experimental challenge of pregnant bison and cattle with *Brucella abortus* strain 2308. *Clinical and Vaccine Immunology* 18(12):2075-2078.
- Olsen, S.C., and C. Johnson. 2012a. Immune responses and safety after dart or booster vaccination of bison with *Brucella abortus* strain RB51. *Clinical and Vaccine Immunology* 19(5):642-648.
- Olsen, S.C., and C.S. Johnson. 2012b. Efficacy of dart or booster vaccination with strain RB51 in protecting bison against experimental *Brucella abortus* challenge. *Clinical and Vaccine Immunology* 19(6):886-890.
- Olsen, S.C., and M.V. Palmer. 2014. Advancement of knowledge of *Brucella* over the past 50 years. *Veterinary Pathology* 51(6):1076-1089.
- Olsen, S.C., T.J. Kreeger, and W. Schultz. 2002. Immune responses of bison to ballistic or hand vaccination with *Brucella abortus* strain RB51. *Journal of Wildlife Diseases* 38(4):738-745.
- Olsen, S.C., A.E. Jensen, W.C. Stoffregen, and M.V. Palmer. 2003. Efficacy of calfhood vaccination with *Brucella abortus* strain RB51 in protecting bison against brucellosis. *Research in Veterinary Science* 74(1):17-22.
- Olsen, S.C., S.J. Fach, M.V. Palmer, R.E. Sacco, W.C. Stoffregen, and W.R. Waters. 2006. Immune responses of elk to initial and booster vaccinations with *Brucella abortus* strain RB51 or 19. *Clinical and Vaccine Immunology* 13(10):1098-1103.
- Olsen, S.C., S.M. Boyle, G.G. Schurig, and N.N. Sriranganathan. 2009. Immune responses and protection against experimental challenge after vaccination of bison with *Brucella abortus* strain RB51 or RB51 overexpressing superoxide dismutase and glycosyltransferase genes. *Clinical and Vaccine Immunology* 16(4):535-540.
- Olsen, S.C., J.L. McGill, R.E. Sacco, and S.G. Hennager. 2015. Immune responses of bison and efficacy after booster vaccination with *Brucella abortus* strain RB51. *Clinical and Vaccine Immunology* 22(4):440-447.
- Palmer, M.V., S.C. Olsen, M.J. Gilsdorf, L.M. Philo, P.R. Clarke, and N.F. Cheville. 1996. Abortion and placentitis in pregnant bison (*Bison bison*) induced by the vaccine candidate, *Brucella abortus* strain RB51. *American Journal of Veterinary Research* 57(11):1604-1607.
- Payne, J.M. 1959. The pathogenesis of experimental brucellosis in the pregnant cow. *Journal of Pathology and Bacteriology* 78:447-463.
- Poester, F.P., L.E. Samartino, and R.L. Santos. 2013. Pathogenesis and pathobiology of brucellosis in livestock. *Revue Scientifique et Technique Office International des Epizooties* 32(1):105-115.
- Qin, Q.M., J. Pei, V. Ancona, B.D. Shaw, T.A. Ficht, and P. de Figueiredo. 2008. RNAi screen of endoplasmic reticulum-associated host factors reveals a role for IRE1alpha in supporting *Brucella* replication. *PLOS Pathogens* 4(7):e1000110.

Revisiting Brucellosis in the Greater Yellowstone Area

- Qureshi, T., J.W. Templeton, and L.G. Adams. 1996. Intracellular survival of *Brucella abortus*, *Mycobacterium bovis* BCG, *Salmonella dublin*, and *Salmonella typhimurium* in macrophages from cattle genetically resistant to *Brucella abortus*. *Veterinary Immunology and Immunopathology* 50:55-65.
- Radhakrishnan, G.K., Q. Yu, J.S. Harms, and G.A. Splitter. 2009. *Brucella* TIR domain-containing protein mimics properties of the toll-like receptor adaptor protein TIRAP. *Journal of Biological Chemistry* 284(15):9892-9898.
- Rajashekara, G., L. Eskra, A. Mathison, E. Petersen, Q. Yu, J. Harms, and G. Splitter. 2006. *Brucella*: Functional genomics and host-pathogen interactions. *Animal Health Research Reviews* 7(1-2):1-11.
- Rhyan, J.C. 2013. Pathogenesis and pathobiology of brucellosis in wildlife. *Revue Scientifique et Technique Office International des Epizooties* 32(1):127-136.
- Rhyan, J.C., W.J. Quinn, L.S. Stackhouse, J.J. Henderson, D.R. Ewalt, J.B. Payeur, M. Johnson, and M. Meagher. 1994. Abortion caused by *Brucella abortus* biovar 1 in a free-ranging bison (*Bison bison*) from Yellowstone National Park. *Journal of Wildlife Diseases* 30(3):445-446.
- Rhyan, J.C., S.D. Holland, T. Gidlewski, D.A. Saari, A.E. Jensen, D.R. Ewalt, S.G. Hennager, S.C. Olsen, and N.F. Cheville. 1997. Seminal vesiculitis and orchitis caused by *Brucella abortus* biovar 1 in young bison bulls from South Dakota. *Journal of Veterinary Diagnostic Investigation* 9(4):368-374.
- Rhyan, J.C., T. Gidlewski, T.J. Roffe, K. Aune, L.M. Philo, and D.R. Ewalt. 2001. Pathology of brucellosis in bison from Yellowstone National Park. *Journal of Wildlife Diseases* 37(1):101-109.
- Rhyan, J.C., K. Aune, T. Roffe, D. Ewalt, S. Hennager, T. Gidlewski, S. Olsen, and R. Clarke. 2009. Pathogenesis and epidemiology of brucellosis in yellowstone bison: Serologic and culture results from adult females and their progeny. *Journal of Wildlife Diseases* 45(3):729-739.
- Rhyan, J.C., P. Nol, C. Quance, A. Gertonson, J. Belfrage, L. Harris, K. Straka, and S. Robbe-Austerman. 2013. Transmission of brucellosis from elk to cattle and bison, Greater Yellowstone area, U.S.A., 2002-2012. *Emerging Infectious Diseases* 19(12):1992-1995.
- Roffe, T.J., S.C. Olsen, T. Gidlewski, A.E. Jensen, M.V. Palmer, and R. Huber. 1999a. Biosafety of parenteral *Brucella abortus* RB51 vaccine bison calves. *Journal of Wildlife Management* 63:950-959.
- Roffe, T.J., J.C. Rhyan, K. Aune, L.M. Philo, D.R. Ewalt, T. Gidlewski, and S.G. Hennager. 1999b. Brucellosis in Yellowstone National Park bison: Quantitative serology and infection. *Journal of Wildlife Management* 63:1132-1137.
- Roffe, T.J., L.C. Jones, K. Coffin, M.L. Drew, S.J. Sweeney, S.D. Hagius, P.H. Elzer, and D. Davis. 2004. Efficacy of single calfhood vaccination of elk with *Brucella abortus* strain 19. *Journal of Wildlife Management* 68(4):830-836.
- Roop, R.M., II, and C.C. Caswell. 2013. Bacterial persistence: Finding the “sweet spot.” *Cell Host and Microbe* 14(2):119-120.
- Rosinha, G.M., D.A. Freitas, A. Miyoshi, V. Azevedo, E. Campos, S.L. Cravero, O. Rossetti, G. Splitter, and S.C. Oliveira. 2002. Identification and characterization of a *Brucella abortus* ATP-binding cassette transporter homolog to *Rhizobium meliloti* ExsA and its role in virulence and protection in mice. *Infection and Immunity* 70(9):5036-5044.
- Rossetti, C.A., C.L. Galindo, H.R. Garner, and L.G. Adams. 2010. Selective amplification of *Brucella melitensis* mRNA from a mixed host-pathogen total RNA. *BMC Research Notes* 3:244.
- Rossetti, C.A., K.L. Drake, and L.G. Adams. 2012. Transcriptome analysis of HeLa cells response to *Brucella melitensis* infection: A molecular approach to understand the role of the mucosal epithelium in the onset of the *Brucella* pathogenesis. *Microbes and Infection* 14(9):756-767.
- Rossetti, C.A., K.L. Drake, P. Siddavatam, S.D. Lawhon, J.E. Nunes, T. Gull, S. Khare, R.E. Everts, H.A. Lewin, and L.G. Adams. 2013. Systems biology analysis of *Brucella* infected Peyer's patch reveals rapid invasion with modest transient perturbations of the host transcriptome. *PLOS ONE* 8(12):e81719.
- Samartino, L.E., and F.M. Enright. 1993. Pathogenesis of abortion of bovine brucellosis. *Comparative Immunology, Microbiology and Infectious Diseases* 16(2):95-101.
- Sankarasubramanian, J., U.S. Vishnu, V. Dinakaran, J. Sridhar, P. Gunasekaran, and J. Rajendhran. 2016. Computational prediction of secretion systems and secretomes of *Brucella*: Identification of novel type IV effectors and their interaction with the host. *Molecular Biosystems* 12(1):178-190.
- Seabury, C.M., N.D. Halbert, P.J. Gogan, J.W. Templeton, and J.N. Derr. 2005. Bison PRNP genotyping and potential association with *Brucella* spp. seroprevalence. *Animal Genetics* 36(2):104-110.
- See, W., W.H. Edwards, S. Dauwalter, C. Almendra, M.D. Kardos, J.L. Lowell, R. Wallen, S.L. Cain, W.E. Holben, and G. Luikart. 2012. *Yersinia enterocolitica*: An unlikely cause of positive brucellosis tests in Greater Yellowstone Ecosystem bison (*Bison bison*). *Journal of Wildlife Diseases* 48(3):537-541.

Scientific Progress and New Research Tools

- Sengupta, D., A. Koblansky, J. Gaines, T. Brown, A.P. West, D. Zhang, T. Nishikawa, S.G. Park, R.M. Roop, II, and S. Ghosh. 2010. Subversion of innate immune responses by *Brucella* through the targeted degradation of the TLR signaling adapter, MAL. *Journal of Immunology* 184(2):956-964.
- Shumaker, B.A., J.A.K. Mazet, B.J. Gonzales, P.H. Elzer, S.K. Hietala, and M.H. Ziccardi. 2010. Evaluation of the western immunoblot as a detection method for *Brucella abortus* exposure in elk. *Journal of Wildlife Diseases* 46(1):87-94.
- Silva, T.M., E.A. Costa, T.A. Paixao, R.M. Tsolis, and R.L. Santos. 2011. Laboratory animal models for brucellosis research. *Journal of Biomedicine and Biotechnology* 2011:518323.
- Smith, J.A., M. Khan, D.D. Magnani, J.S. Harms, M. Durward, G.K. Radhakrishnan, Y.P. Liu, and G.A. Splitter. 2013. *Brucella* induces an unfolded protein response via TcpB that supports intracellular replication in macrophages. *PLOS Pathogens* 9(12):e1003785.
- Stevens, M.G., S.C. Olsen, and N.F. Cheville. 1995. Comparative analysis of immune responses in cattle vaccinated with *Brucella abortus* strain 19 or strain RB51. *Veterinary Immunology and Immunopathology* 44(3-4):223-235.
- Sweeney, S.J., C. Emerson, and I.S. Eriks. 2001. Cloning, sequencing, and expression of interferon-gamma from elk in North America. *Journal of Wildlife Diseases* 37(1):164-171.
- Thorne, E.T., and J.K. Morton. 1978. Brucellosis in elk. II. Clinical effects and means of transmission as determined through artificial infections. *Journal of Wildlife Diseases* 14(3):280-291.
- Thorne, E.T., T.J. Kreeger, T.J. Walthall, and H.A. Dawson. 1981. Vaccination of elk with strain 19 *Brucella abortus*. *Proceedings of the U.S. Animal Health Association* 85:359-374.
- Tiwari, A., P. Afley, D.K. Sharma, C.S. Bhatnagar, B. Bhardwaj, G.P. Rai, and S. Kumar. 2014. Real-time PCR carried out on DNA extracted from serum or blood sample is not a good method for surveillance of bovine brucellosis. *Tropical Animal Health and Production* 46(8):1519-1522.
- Tobias, L., D.O. Cordes, and G.G. Schurig. 1993. Placental pathology of the pregnant mouse inoculated with *Brucella abortus* strain 2308. *Veterinary Pathology* 30(2):119-129.
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2003. Brucellosis Eradication: Uniform Methods and Rules, Effective October 1, 2003. APHIS 91-45-013. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/umr_bovine_bruc.pdf (accessed January 6, 2017).
- USDA-APHIS. 2014. Standard Operating Procedures for Submission and Testing of Brucellosis Serological Specimens. APHIS/Veterinary Services Approved Brucellosis Laboratories. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/aphis_approved_br_sero_labs_sop.pdf (accessed January 6, 2017).
- Van Campen, H., and J. Rhyan. 2010. The role of wildlife in diseases of cattle. *Veterinary Clinics of North America: Food Animal Practice* 26(1):147-161.
- Van Houten, C.K., E.L. Belden, T.J. Kreeger, E.S. Williams, W.H. Edwards, E.T. Thorne, W.E. Cook, and K.W. Mills. 2003. Validation of a *Brucella abortus* competitive enzyme-linked immunosorbent assay for use in Rocky Mountain elk (*Cervus Elaphus Nelsoni*). *Journal of Wildlife Diseases* 39(2):316-322.
- Viadas, C., M.C. Rodriguez, F.J. Sangari, J.P. Gorvel, J.M. Garcia-Lobo, and I. Lopez-Goni. 2010. Transcriptome analysis of the *Brucella abortus* BvrR/BvrS two-component regulatory system. *PLOS ONE* 5(4):e10216.
- Vishnu, U.S., J. Sankarasubramanian, P. Gunasekaran, and J. Rajendhran. 2015. Novel vaccine candidates against *Brucella melitensis* identified through reverse vaccinology approach. *OMICS* 19(11):722-729.
- von Barga, K., J.P. Gorvel, and S.P. Salcedo. 2012. Internal affairs: Investigating the *Brucella* intracellular lifestyle. *FEMS Microbiology Reviews* 36(3):533-562.
- Wang, F., S. Hu, W. Liu, Z. Qiao, Y. Gao, and Z. Bu. 2011. Deep-sequencing analysis of the mouse transcriptome response to infection with *Brucella melitensis* strains of differing virulence. *PLOS ONE* 6(12):e28485.
- Wang, Y., Y. Ke, Z. Wang, X. Yuan, Y. Qiu, Q. Zhen, J. Xu, T. Li, D. Wang, L. Huang, and Z. Chen. 2012. Genome sequences of three live attenuated vaccine strains of *Brucella* species and implications for pathogenesis and differential diagnosis. *Journal of Bacteriology* 194(21):6012-6013.
- Weeks, J.N., C.L. Galindo, K.L. Drake, G.L. Adams, H.R. Garner, and T.A. Ficht. 2010. *Brucella melitensis* VjbR and C12-HSL regulons: Contributions of the N-dodecanoyl homoserine lactone signaling molecule and LuxR homologue VjbR to gene expression. *BMC Microbiology* 10:167.
- Westhusin, M.E., T. Shin, J.W. Templeton, R.C. Burghardt, and L.G. Adams. 2007. Rescuing valuable genomes by animal cloning: A case for natural disease resistance in cattle. *Journal of Animal Science* 85:138-142.
- Williams, E.S., E.T. Thorne, S.L. Anderson, and J.D. Herriges, Jr. 1993. Brucellosis in free-ranging bison (*Bison bison*) from Teton County, Wyoming. *Journal of Wildlife Diseases* 29(1):118-122.

Revisiting Brucellosis in the Greater Yellowstone Area

- Xavier, M.N., T.A. Paixao, F.P. Poester, A.P. Lage, and R.L. Santos. 2009. Pathological, immunohistochemical and bacteriological study of tissues and milk of cows and fetuses experimentally infected with *Brucella abortus*. *Journal of Comparative Pathology* 140(2-3):149-157.
- Xavier, M.N., T.A. Paixão, A.B. den Hartigh, R.M. Tsois, and R.L. Santos. 2010. Pathogenesis of *Brucella* spp. *The Open Veterinary Science Journal* 4:109-118.
- Xavier, M.N., M.G. Winter, A.M. Spees, K. Nguyen, V.L. Atluri, T.M. Silva, A.J. Baumler, W. Muller, R.L. Santos, and R.M. Tsois. 2013. CD4⁺ T cell-derived IL-10 promotes *Brucella abortus* persistence via modulation of macrophage function. *PLOS Pathogens* 9(6):e1003454.

5

Federal, State, and Regional Management Efforts

1. BRIEF HISTORICAL OVERVIEW OF BRUCELLOSIS CONTROL EFFORTS

In 1934, as part of an economic recovery program during the Great Depression to reduce the cattle population, efforts were initiated by the U.S. Department of Agriculture (USDA) to eradicate brucellosis caused by *Brucella abortus* in the United States. This was seen as an opportunity to address the most significant livestock disease problem facing the country at that time, with brucellosis affecting 11.5% of adult cattle in 1934 and 1935 (Ragan, 2002). Recognizing the magnitude of the negative economic impact of brucellosis on the cattle industry and on human health, the U.S. Congress appropriated funds in 1954 for a comprehensive national effort to eradicate brucellosis. The brucellosis eradication program required cooperation between federal agencies, states, and livestock producers (Ragan, 2002). The eradication program has been modified several times since then as the science and technology of brucellosis has developed over the years through research and experience. There were a number of key developments that were major turning points in the program. Some of these were advances in technology, while others were procedures learned through trial and error (Ragan, 2002). The brucellosis eradication program made tremendous progress, resulting in a dramatic decrease in brucellosis-affected cattle herds in the United States over time. At the end of 2001, for the first time in the United States, there were no known brucellosis-affected herds remaining (USAHA, 2001). The number of human brucellosis cases also declined steadily over the course of the brucellosis eradication program. There are now only about 100 cases of human brucellosis reported per year, most often associated with travelers who have consumed unpasteurized milk and milk products abroad that were infected with *B. melitensis* (Glynn and Lynn, 2008).

2. CHANGES IN STATUS AND CLASSIFICATION OF STATES

Brucellosis regulations have provided a system of classifying states or areas within states based on incidence of findings of brucellosis in cattle or privately owned bison herds within the state or area (9 CFR Part 78). The classifications are Class Free, Class A, Class B, and Class C. As each state moves or approaches Class Free status, restrictions on interstate movement of cattle and domestic bison become less stringent. The achievement of Class Free status has historically been based on the finding of no *B. abortus*-infected herds within the state or area within 12 months preceding classification as Class Free, with documentation of adequate surveillance. Maintenance of Class Free status by states or areas requires surveillance through biannual ring testing at dairies and slaughter surveillance from at least 95% of all cows and bulls 2 years of age or over at each recognized slaughtering establishment.

In 1997, the Brucellosis Emergency Action Plan was initiated and it emphasized rapid response, enhanced surveillance, epidemiology and herd management, and depopulating affected herds. All activities involving new cases of brucellosis and brucellosis surveillance were handled as a top priority. As part of the new emphasis, herds identified with brucellosis in a Class Free state had to be depopulated within 60 days of diagnosis in order for that state to continue to be designated as Class Free. Two herds diagnosed with brucellosis in any 24-month period was cause for downgrade to Class A status.

Revisiting Brucellosis in the Greater Yellowstone Area

In February 2008, every state, along with the territories of Puerto Rico and the Virgin Islands, achieved Class Free State status for the first time in the 74-year history of the U.S. brucellosis program. This accomplishment was short-lived, however, as Montana lost its Class Free status in September 2008 after two brucellosis-affected cattle herds were found within 1 year. Recognizing the success of the Brucellosis Eradication Plan across the United States, and that the last known wildlife reservoir of *B. abortus* exists in the bison and elk populations in the Greater Yellowstone Area (GYA), USDA's Animal and Plant Health Inspection Service (USDA-APHIS) determined that a new direction was necessary to allow Veterinary Services and the states to apply limited resources effectively and efficiently to this disease risk (USDA-APHIS, 2009).

In 2010, USDA-APHIS published an interim rule that made several changes to the regulations consistent with the goal of shifting resources to more efficiently address *B. abortus* control and eradication in the domestic livestock population. States that had been classified as brucellosis Class Free for 5 or more years now maintain status without Brucellosis Milk Ring Surveillance (BMST), and slaughter surveillance nationwide has been significantly reduced. Instead of depopulating herds, states or areas can maintain Class Free status while managing herds affected with brucellosis under quarantine with an approved herd plan.

Under the interim rule, specific requirements are imposed on states with infected wildlife reservoirs to ensure that the spread of *B. abortus* between wildlife and livestock is mitigated. The rule also moved away from requirements for automatic status downgrades in states when two or more herds are identified with brucellosis within 24 months or if an infected herd is not depopulated within 60 days. Instead, USDA-APHIS allows states to maintain Class Free status if the state makes appropriate disposition of any affected herds and conducts surveillance "adequate to detect brucellosis if it is present in other herds or species" (USDA-APHIS, 2010).

3. REGIONAL AND NATIONAL CONTROL PROGRAMS

USDA-APHIS has the regulatory authority to manage animal diseases in livestock. However, brucellosis in the GYA is complicated by the fact that there are a multitude of federal and state agencies involved, with differing mandates, management responsibilities, and authorities. Although regulated livestock disease programs generally fall under USDA-APHIS and state animal health agencies, wildlife are managed by state wildlife agencies and the U.S. Department of the Interior (DOI). Thus, USDA-APHIS cooperates with state wildlife management agencies in the management of wildlife diseases and with state animal health and livestock agencies in the management of livestock diseases. Management of national parks falls under the purview of the National Park Service (USDOI and USDA, 2000).

3.1 Involvement of Federal Agencies

Within the boundaries of Yellowstone National Park (YNP), the Secretary of the Interior has exclusive jurisdiction to manage the Park's natural resources, including bison and elk (USDOI and USDA, 2000). When the bison and elk are outside of YNP on National Forest Service lands, the U.S. Forest Service (USFS) has responsibilities under federal laws to provide habitat for wildlife. Federal law also requires USDA-APHIS to control and prevent the spread of communicable and contagious diseases of livestock. Therefore, depending on what lands the bison or elk are located on, management responsibilities and authorities differ and change when wildlife cross certain boundaries. Table 5-1 below illustrates federal agency jurisdiction and involvement.

TABLE 5-1 Federal Agency Jurisdiction and Involvement in Brucellosis

Federal Agency	Mission	Relevant Jurisdiction	GYA Involvement
USDA: Animal and Plant Health Inspection Service	To protect the health and value of American agriculture and natural resources.	Federal law requires APHIS to control and prevent the spread of communicable and contagious diseases of livestock.	<ul style="list-style-type: none">• The objective of the national brucellosis program: eradicate brucellosis from the United States so it no longer poses a threat to domestic livestock, wildlife, and public health.• Three main objectives:<ul style="list-style-type: none">(1) safeguard the health of livestock;(2) maintain the economic viability and trade capabilities of the U.S. cattle industry; and(3) protect public health and food safety.
USDA: U.S. Forest Service	To sustain the health, diversity, and productivity of the nation's forests and grasslands to meet the needs of present and future generations.	When the bison are on national forest system lands, the U.S. Forest Service has responsibilities under federal laws to provide habitat for the bison, a native species.	<ul style="list-style-type: none">• Of the GYA, 48% is National Forest Service lands and 15% is Bridger-Teton National Forest.• Recognize the role of the states to manage wildlife and fish populations within their jurisdictions and the responsibility of the U.S. Fish & Wildlife Service to manage fish and wildlife resources within its authority.• Forest Plan Goals which are potentially pertinent to the current discussion include:<ul style="list-style-type: none">(1) Supporting community prosperity through authorization of livestock grazing.(2) Providing habitat to support populations of game and fish.(3) Supporting community prosperity through re-establishing historic elk migration routes.• The elk feedgrounds located on NFS lands are authorized through a special use permit.
DOI: National Park Service– Yellowstone National Park (YNP)	To preserve unimpaired the natural and cultural resources and values of the National Park System for the enjoyment, education, and inspiration of this and future generations. The Park Service cooperates with partners to extend the benefits of natural and cultural resource conservation and outdoor recreation throughout this country and the world.	Within the boundaries of YNP, the Secretary of the Interior has exclusive jurisdiction to manage the parks natural resources, including bison and elk.	<ul style="list-style-type: none">• Manage bison, elk, and other wildlife within YNP.• In the late 1960s, the National Park Service decided to end the direct management of the bison herd to allow natural forces to affect and determine the herd size. Since then, the herd has increased from nearly 400 to more than 4,000.• Bison currently regulated between 3,000 and 5,000.• Elk population about 5,000.
DOI: National Park Service– Grand Teton National Park (GTNP)	To preserve unimpaired the natural and cultural resources and values of the National Park System for the enjoyment, education, and inspiration of this and future generations. The Park Service cooperates with partners to extend the benefits of natural and cultural resource conservation and outdoor recreation throughout this country and the world.	Within the boundaries of GTNP, the Secretary of the Interior has exclusive jurisdiction to manage the parks natural resources, including bison and elk.	<ul style="list-style-type: none">• Protect wildlands and wildlife habitat within the GYA, including a program for the permanent conservation of elk within the park.• Includes “controlled reduction of elk...when found necessary” by NPS and the Wyoming Game and Fish Commission.• February 2015 bison count: 691. High % seropositive for brucellosis.• Allows some grazing leases.

continued

TABLE 5-1 Continued

Federal Agency	Mission	Relevant Jurisdiction	GYA Involvement
DOI: U.S. Fish & Wildlife Service, National Elk Refuge	Working with others to conserve, protect, and enhance fish, wildlife, plants, and their habitats for the continuing benefit of the American people.	The National Elk Refuge provides, preserves, restores, and manages winter habitat for the nationally significant Jackson elk herd as well as habitat for endangered species, birds, fish, and other big game animals.	<ul style="list-style-type: none">• There are an estimated 11,000 elk in the Jackson elk herd. The elk migrate across several jurisdictional boundaries, including the National Elk Refuge, Grand Teton National Park, John D. Rockefeller, Jr. Memorial Parkway, Yellowstone National Park, Bridger-Teton National Forest, Bureau of Land Management resource areas, and state and private lands. Elk use extensive spring, summer, and fall ranges to the northwest and east of the refuge and as far away as southern YNP. Summer distribution of the Jackson herd is estimated to be approximately 30% Grand Teton National Park, 30% Gros Ventre, 25% YNP, and 15% Teton Wilderness.• Most of the Jackson bison herd winters on the refuge but are in areas where they cannot be easily viewed by the public. During the summer, bison primarily use nonforested areas of grassland and sage-steppe in Grand Teton National Park. In spring and fall transitional periods, bison may be found throughout both summer and winter range.
DOI: Bureau of Land Management	To sustain the health, diversity, and productivity of America's public lands for the use and enjoyment of present and future generations.	Administer grazing permits and leases for livestock on BLM managed land.	<ul style="list-style-type: none">• Administer 18,000 grazing permits and leases for livestock on more than 21,000 allotments across the nation under BLM management.

SOURCES: USDOI and USDA, 2000; USDA-APHIS, 2015; BLM, 2016; FWS, 2016a,b,c,d; NPS, 2016a; USFS, 2016.

*Federal, State, and Regional Management Efforts***3.2 Involvement of State Agencies**

The Idaho State Department of Agriculture, the Wyoming Livestock Board, and the Montana Department of Livestock each have authority and responsibility for livestock disease control and eradication, regulation of livestock importation into the state, and protection of the livestock interests of the state. The mission of the Montana Department of Livestock also includes the responsibility to prevent the transmission of animal diseases to humans. The agencies are also responsible for overseeing brucellosis surveillance in livestock, managing the risk of brucellosis to livestock in the GYA, and prevention and response efforts to any brucellosis outbreaks in livestock in their respective states. Furthermore, the agencies are responsible for the designation of and management of the brucellosis designated surveillance areas (DSAs) in their respective states.

The Idaho Department of Fish and Game (IDFG), the Wyoming Game & Fish Department (WGFD), and the Montana Department of Fish, Wildlife & Parks (MFWP) are responsible for wildlife management in their respective states, including preserving and protecting wildlife and managing wildlife hunting. Table 5-2 illustrates state agency jurisdiction and involvement.

Test and Remove Pilot Program in Elk

Since 1912, the U.S. Fish & Wildlife Service (USFWS) has implemented a supplemental feeding program on the National Elk Refuge (NER) for the purpose of sustaining elk populations, reducing winter mortality, and reducing crop damages on private lands. The same rationale was cited by WGFD for commencing a supplemental feeding program in 1929. Today, between 20,000 and 25,000 elk are fed annually along the 22 feedgrounds in western Wyoming (in Lincoln, Sublette, and Teton Counties) and the NER (Scurlock et al., 2010).

WGFD implemented a \$1.2 million pilot project occurring over a 5-year span to reduce brucellosis prevalence in elk. From 2006-2010, a test-and-remove strategy targeted three feedgrounds in the Pinedale elk herd unit. This pilot project was endorsed by the Wyoming Brucellosis Coordination Team (WBCT) and conducted in response to a goal of reducing seroprevalence and eventually eliminating brucellosis in wildlife, specifically addressing winter elk feedgrounds (WBCT, 2005). Male elk were not targeted due to their insignificance in brucellosis transmission. Although at least two trapping attempts were conducted every year, only 49% of adult and yearling female elk available were captured and tested. Brucellosis seroprevalence reductions were also observed on the two other feedgrounds included in the study (Scurlock et al., 2010).

During the pilot project, the seroprevalence of *B. abortus* decreased significantly in elk captured at the Muddy Creek feedground: from 37% in 2006 to 5% in 2010 (Scurlock et al., 2010) (see Figure 5-1). In 2007, seropositive elk that were also culture positive ranged from 36% in Scab Creek to 77% at Muddy Creek. The results of this pilot project showed reduced seroprevalence by more than 30 percentage points in 5 years as a result of capturing nearly half of available yearling and adult female elk attending a feedground and removing those that tested seropositive. Seroprevalence trends on other state feedgrounds did not result in a similar decrease in seroprevalence, which indicates that removing seropositive individuals reduces prevalence beyond natural oscillations (Scurlock et al., 2010). Although the seroprevalence was significantly reduced, brucellosis transmission events were not disrupted because only half of the elk were captured. After the 5-year pilot project was discontinued, the seroprevalence of brucellosis in elk on the feedgrounds resurged.

TABLE 5-2 State Agency Jurisdiction and Involvement in Brucellosis

State Agency	Mission (Relevant Sections)	GYA Involvement
Idaho State Department of Agriculture	<ul style="list-style-type: none">• Disease control and eradication.• Maintaining an animal disease-free status for the state.• Inspection and testing of animals, milk, and milk products.• Enhancing the viability of rural communities by providing leadership in managing Idaho’s natural resources and assistance in resolving rangeland management issues.	Oversees administration of the designated surveillance areas (DSAs) in Idaho. Responsible for brucellosis control and eradication in livestock.
Montana Department of Livestock	To control and eradicate animal diseases, prevent the transmission of animal diseases to humans, and to protect the livestock industry from theft and predatory animals.	Oversees administration of the DSA in Montana. Responsible for brucellosis control and eradication in livestock.
Wyoming Livestock Board	“The Wyoming Livestock Board Animal Health Unit exercises general supervision over and protection of the livestock interests of the state from disease by implementing board rules and regulations, assisting in enforcement, monitoring the import of livestock and biologic agents into the state and disseminating lawful and accurate information.”	Oversees administration of the DSA in Wyoming. Responsible for brucellosis control and eradication in livestock.
Idaho Department of Fish and Game	“All wildlife, including all wild animals, wild birds, and fish, within the state of Idaho, is hereby declared to be the property of the state of Idaho. It shall be preserved, protected, perpetuated, and managed. It shall be only captured or taken at such times or places, under such conditions, or by such means, or in such manner, as will preserve, protect, and perpetuate such wildlife, and provide for the citizens of this state and, as by law permitted to others, continued supplies of such wildlife for hunting, fishing and trapping.”	Works to maintain or improve game populations to meet the demand for hunting. Works to reduce or eliminate the risk of transmission of disease between captive in free ranging wildlife. Collaborates with other agencies and education institutions on disease control, prevention, and research.
Wyoming Game & Fish Department	Provides an adequate and flexible system of control, propagation, management, and protection and regulation of all wildlife in Wyoming.	Manages 22 state-operated elk feedgrounds in Wyoming. Also oversees Brucellosis Management Action Plans (BMAPs) for elk herds as well as the Jackson bison herd and the Absaroka bison herd.
Montana Fish, Wildlife & Parks	Provides for the stewardship of the fish, wildlife, parks, and recreational resources of Montana while contributing to the quality of life for present and future generations.	Administers elk management plans in Montana. Conducts and participates in research projects related to brucellosis in elk.

SOURCES: IDFG, 2015, 2016; MFWP, 2016a,b; WGFD, 2016a,b; Wyoming Livestock Board, 2016.

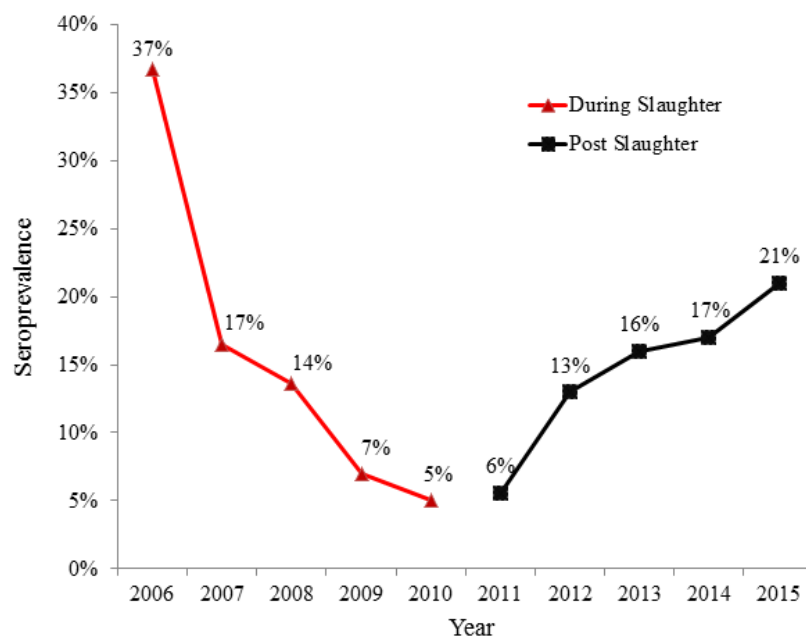
Federal, State, and Regional Management Efforts

FIGURE 5-1 Seroprevalence of *B. abortus* in elk by year for test and slaughter pilot project at Muddy Creek Feedground. Pilot was discontinued after 5 years and seroprevalence resurged. SOURCE: Scurlock et al., 2010.

Use of Feedgrounds for Separating Cattle from Elk

Although elk are currently considered one of the primary reservoirs of *B. abortus*, feedgrounds serve as a primary method to maintain separation of elk and livestock and prevent intraspecies transmission of brucellosis (Maichak et al., 2009). In Wyoming alone, 22 elk feedgrounds and the NER support up to 25,000 elk (Maichak et al., 2009). With brucellosis transmitted from elk to cattle in the GYA (Rhyan et al., 2013), minimizing contact between the two species on feedgrounds has become even more important. There is the perception that feedgrounds reduce the risk of interspecies brucellosis by separating elk and domestic cattle. However, several cases of brucellosis have been discovered in cattle near feedgrounds (FWS, 2016d).

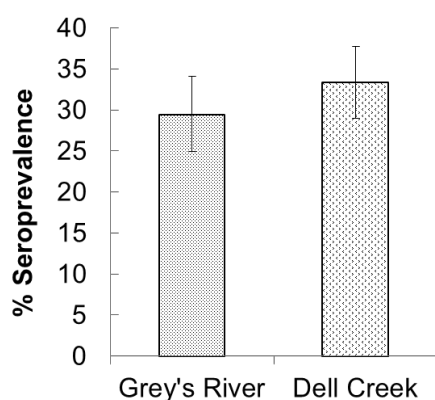
Vaccination of Elk on Wyoming Feedgrounds

Vaccination of wildlife has been shown to reduce and in some cases eliminate diseases from host wildlife populations (Plumb et al., 2007). Oral rabies vaccine (ORV) in wildlife has been used in several European countries to successfully eliminate rabies in red foxes (*Vulpes vulpes*). In the United States, the integration of ORV into the dog vaccination program was a major factor leading to the country's canine-rabies-free status, which was declared in 2007 based on World Health Organization standards (Slate et al., 2009).

In 1985, a *Brucella abortus* strain 19 (S19) vaccination program began on the elk feedgrounds in Wyoming due to a high seroprevalence of brucellosis in elk. S19 was delivered via biobullet to animals frequenting the feedgrounds (Scurlock, 2015). From 1985–2015, approximately 91,145 juvenile elk (99% average vaccinated per year) and 19,336 adults (6% average vaccinated per year) were vaccinated with S19 (Scurlock, 2015). In comparing the seroprevalence of feedground elk before and after vaccination, there are no relevant effects of vaccination (see Figure 5-2). In addition, the amount of vaccination coverage at a feedground did not correlate with reduced seroprevalence after accounting for confounding factors. Finally, the seroprevalence at vaccinated feedgrounds was not demonstrably lower than a non-vaccinated feedground (Maichak et al., 2017).

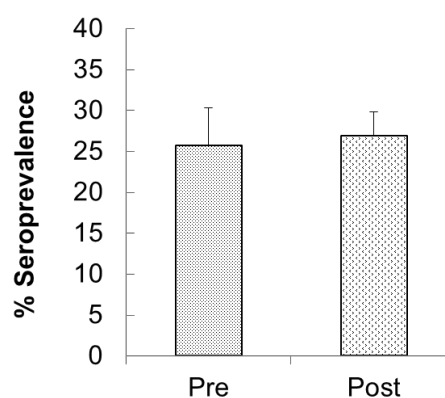
Revisiting Brucellosis in the Greater Yellowstone Area

Vaccinated vs. Unvaccinated



One-Tailed t-Test: $p = 0.27$

Pre-Vaccination vs. Post-Vaccination



One-Tailed t-Test: $p = 0.47$

FIGURE 5-2 Efficacy of elk *Brucella* strain 19 vaccination. SOURCE: Scurlock, 2015.

Numerous studies have been conducted to evaluate the efficacy of S19 in elk relative to protection from abortion and or infection. In a controlled challenge study, S19 vaccine provided low protection against abortion and no protection from infection (Roffe et al., 2004). In addition, single abortions on feedgrounds may expose many elk, and individual elk could receive multiple exposures from more than one fetus. Therefore, a naturally acquired challenge dose for exposed animals could easily and realistically be much higher than an experimental challenge dose (Roffe et al., 2004). A single calfhood vaccination of elk with S19 produces a very low level of immunity in vaccinated elk and would be highly unlikely to lead to significant reduction or eradication of brucellosis from feedground elk (Roffe et al., 2004). However, other challenge studies have indicated that S19 provided modest protection against reproductive failures (Thorne et al., 1981; Herriges et al., 1989).

One possible reason for the inconsistent findings relative to S19 efficacy in various experimental and field conditions may be related to frequent and highly concentrated exposure to fetal abortion materials (such as tissues and fluids) on feedgrounds. Two factors appear to drive the transmission of *B. abortus*: there are massive amounts of *B. abortus* present in the placental fluids and general exudates from the aborting female, combined with the strong attractant effect of expelled fetal membranes (NRC, 1998). Elk-fetus contact levels were highest when fetuses were placed on traditional feedlines (Maichak et al., 2009). Recent fetal contact studies on an elk feedground have shown that more than 30% of a population can be exposed to one fetus or abortion within 24 hours (Creech et al., 2012). This high rate of exposure to aborted materials minimizes the effect of vaccination as the likelihood of infection is related to the dosage of the infectious challenge, and each gram of aborted material tissues typically has billions of *Brucella* organisms (Enright, 1990).

In 2013, SolidTech Animal Health, Inc., the sole producer of biobullets and projectors, terminated their ballistic technologies division and had not sold the rights or equipment to produce biobullets (Scurlock, 2015; Maichak et al., 2017). Therefore, remote vaccination of elk with S19 vaccine is no longer an option for managers at this time.

4. INTERAGENCY COOPERATIVE BODIES

Several cooperative state and federal interagency bodies were developed to address brucellosis-specific issues in the GYA: the Greater Yellowstone Interagency Brucellosis Committee (GYIBC), the Interagency Bison Management Plan (IBMP), and WBCT.

Federal, State, and Regional Management Efforts

4.1 Greater Yellowstone Interagency Brucellosis Committee

GYIBC was formed in 1995 through a memorandum of agreement signed by the Secretaries of Agriculture and of the Interior and by the governors of Idaho, Montana, and Wyoming (Brunner et al., 2002). The GYIBC consisted of an executive committee, two subcommittees, a technical subcommittee, and an information and education subcommittee (NPS, 2016b). Governmental representatives to the committee included the state veterinarians and directors of state wildlife agencies from the states of Idaho, Montana, and Wyoming. Federal voting members of the GYIBC executive committee included USDA-APHIS Veterinary Services, USDA Forest Service, the National Park Service (DOI), U.S. Fish & Wildlife Service (DOI), and the Bureau of Land Management (BLM). There were also three nonvoting members represented on the GYIBC committee: the U.S. Geological Survey, USDA's Agricultural Research Service, and the InterTribal Bison Cooperative (OMB, 2007).

The goal of the GYIBC was to protect and sustain the existing free-ranging elk and bison populations in the GYA and to protect the public interests and economic viability of the livestock industry in Idaho, Montana, and Wyoming (GYIBC, 2005). Toward this end, the mission of the GYIBC facilitated the development and implementation of brucellosis management plans for elk and bison in the GYA (GYIBC, 2005).

The GYIBC had a number of management objectives intended to guide their activities (GYIBC, 2005):

- Recognize and maintain existing state and federal jurisdictional authority for elk, bison, and livestock in the GYA;
- Maintain numerically, biologically, and genetically viable elk and/or bison populations in the respective states, national parks, and wildlife refuges;
- Maintain the brucellosis-free status of Idaho, Montana, and Wyoming and protect the ability of producers in the respective states to freely market livestock;
- Eliminate brucellosis-related risks to public health;
- Eliminate the potential transmission of *B. abortus* among elk, bison, and livestock;
- Coordinate brucellosis-related management activities among all affected agencies;
- Base brucellosis-related management recommendations on defensible and factual information while encouraging and integrating new advances and technology;
- Aggressively seek public involvement in the decision-making process;
- Communicate to the public factual information about the need to prevent the transmission of brucellosis, the need for its eradication, and the rationale for related agency management actions; and
- Plan for elimination of *B. abortus* from the GYA by the year 2010.

In May 2005, after the GYIBC memorandum of understanding (MOU) expired, USDA and DOI agreed on a revised GYIBC MOU and presented the draft to the governors of Idaho, Montana, and Wyoming for consideration (U.S. Congress, 2007). The revised MOU was ultimately not signed by the governors, and the GYIBC was disbanded.

4.2 Interagency Bison Management Plan

The IBMP was developed to address the issue of bison exiting YNP and entering the state of Montana. Signed in 2000, the IBMP was a result of federal and state agencies recognizing that a coordinated, cooperative management regime was necessary for providing consistency and reliability to the process of managing bison that move from YNP into Montana. This interagency management plan resulted from 10 years of mediated negotiations in Montana between agencies to come to agreement. The IBMP was strictly a plan to manage bison that exit YNP and enter the state of Montana. It was not intended to be a brucellosis eradication plan; rather it was meant to be a means to manage bison and cattle to minimize the risk of interspecies transmission. The IBMP also states that “these management actions demonstrate a long-term

Revisiting Brucellosis in the Greater Yellowstone Area

commitment by the agencies to work towards the eventual elimination of brucellosis in free ranging bison in Yellowstone National Park” (USDOI and USDA, 2000).

Specifically, the IBMP seeks to (IBMP, 2016):

- Maintain a wild, free-ranging bison population;
- Reduce the risk of brucellosis transmission from bison to cattle;
- Manage bison that leave YNP and enter the state of Montana; and
- Maintain Montana’s brucellosis-free status for domestic livestock.

The IBMP has been effective in maintaining the separation of bison and cattle, and there is no evidence that there has been transmission of brucellosis from wild bison to cattle in the GYA since the IBMP was implemented. Management of elk was outside the scope the IBMP negotiated agreement (USDOI and USDA, 2000). The IBMP is evaluated regularly and modified as needed through adaptive management.

4.3 Wyoming Brucellosis Coordination Team

The WBCT was created in 2004 by the governor of Wyoming to address the issue of brucellosis for Wyoming. The impetus for the formation of the WBCT resulted from a case of brucellosis in a herd of cattle from Sublette County, Wyoming. This case is believed to be the result of contact with infected elk from the nearby Muddy Creek elk feedground area (Galey, 2015). The WBCT included 19 members and 10 technical advisors, including sportsmen, outfitters, ranchers, state, university, legislators, federal managers, and representatives from the governor’s office (Galey, 2015).

The WBCT was tasked “with identifying issues, describing best management practices, and developing recommendations related to brucellosis in wildlife and livestock in the state” (WBCT, 2005). It was also asked to provide recommendations that detail actions, responsibilities, and timetables where appropriate. In 2005, the WBCT presented a report to the governor of Wyoming that contained 28 specific recommendations for action under four topic areas (WBCT, 2005). The four topics include “(1) reclaiming Class-Free brucellosis status for cattle, surveillance, and transmission between species; (2) developing an Action Plan of what to do in the event of a new case in cattle; (3) addressing human health concerns; and (4) reducing and eventually eliminating brucellosis in wildlife, specifically addressing winter elk feedgrounds” (WBCT, 2005). Many of the recommended measures have been implemented, and the WBCT continues to meet biannually to combine efforts of agencies, landowners, and others to move the Wyoming brucellosis management issue forward.

5. SURVEILLANCE

5.1 National Surveillance for Brucellosis

The Market Cattle Identification (MCI) surveillance program was formerly comprised of samples collected from at least 95% of test-eligible adult dairy and beef cattle presented for slaughter at all state and federally recognized slaughter establishments, as well as from adult cattle offered for sale at livestock auction markets. This surveillance stream provided a 99% confidence level that the prevalence of brucellosis was less than one infected animal per one million animals (0.0001%) in the national herd (USDA-APHIS, 2010). This MCI surveillance was supplemented by BMST of dairy herds. In states officially declared free of brucellosis, BMST was required two times per year in commercial dairies and four times per year in states not officially free of brucellosis. The development of this surveillance system was no small undertaking and required ample federal funding to maintain state and federal staffing at levels that would facilitate the cooperation and coordination of sample collection and testing. State-federal cooperative brucellosis laboratories in each state were staffed, equipped, and supplied to accomplish these goals. Annual reporting by states contributed to the information USDA-APHIS used to designate each state’s status.

Federal, State, and Regional Management Efforts

USDA-APHIS began looking at changes to the National Brucellosis Surveillance program as more states achieved and maintained freedom from brucellosis. The agency recognized that the MCI and BMST surveillance systems may no longer be necessary, particularly as many states had been free of the disease for 5 or more years.

Nearly 5.3 million head of cattle were tested under the MCI in FY 2011. This included 4.1 million head tested at slaughter and 1.2 million tested at livestock markets (Carter, 2012). Changes were made to the national slaughter surveillance program beginning in 2011 consistent with the publication of the 2010 interim rule, including a reduction in sample collection at slaughter to approximately 3 million samples. Target sampling numbers were further reduced to 1 million samples in 2012 due to budgetary concerns (Carter, 2013). In FY2014, USDA-APHIS reported approximately 2 million samples collected at slaughter and 97,000 tested at livestock auction markets (Belfrage, 2015).

Only 10 slaughter plants across the nation now participate in sample collection for brucellosis surveillance (see Table 5-3). This level of surveillance is currently designed to detect brucellosis at a prevalence not to exceed 1 infected animal per 100,000 animals, with no disease detected or documented at that level (Belfrage, 2015). However, this surveillance system is not designed to detect brucellosis in animals leaving the DSA for slaughter. Each GYA state has a requirement for testing animals that leave the DSA for purposes of slaughter. The age at which animals are to be tested varies by state, from 12-18 months. Some variation also exists in the GYA state exemptions to testing DSA livestock leaving the DSA if they are destined for a livestock auction market, where it is assumed they will be tested prior to being sold to slaughter, which unfortunately is not always the case.

The 2010 interim rule requires states with a wildlife reservoir of *B. abortus* (in other words, the GYA states) to continue testing all adult cattle at slaughter, which includes adult cattle both within and outside of the DSAs. One of the flaws in this policy is that there are no major adult cattle slaughter plants in Wyoming or Montana, and there is only one slaughter plant in Idaho that is classified as a “top-40” plant by number of cows slaughtered in the United States.¹ No major slaughter capacity for cattle exists in the GYA largely because of the distance from feed sources and feedyards.

Adult cattle that are culled from breeding herds are often transported from Idaho, Montana, and Wyoming to livestock auction markets in neighboring states where routine brucellosis testing is not conducted. Auction markets in South Dakota, for example, receive cull cows and bulls from Montana and Wyoming as they move from the rangelands of the west to feedyards near cornfields to the east and south. These cattle are identified with a backtag reflecting the state of the livestock market—not the state of origin—although traceability information is expected to be in place to allow tracing of an official identification device per the Animal Disease Traceability rule (2012/9CFR). These animals are no longer tested at the auction market and are delivered to slaughter plants across the country, most of which do not participate in the national slaughter surveillance program. This scenario creates a void of surveillance information that represents an at-risk population of cattle outside the boundaries of the DSAs.

5.2 Designated Surveillance Areas

The concept of zoning or regionalization for a disease is an effort to reduce the economic impact to the smallest, appropriate, and manageable geographic area. The World Organisation for Animal Health (OIE) recognizes this approach when considering trade implications related to disease status. Idaho, Montana, and Wyoming began using DSAs when USDA-APHIS drafted a paper outlining a concept for a new regulatory control approach (USDA-APHIS, 2009). As the 2010 interim rule was implemented, all three states developed DSAs based on past surveillance in wildlife as well as the locations of recent bovine cases of brucellosis.

¹Large slaughter establishments are responsible for a majority of the slaughter conducted in the United States. In addition, large slaughter establishments are almost universally specialized to process only one of two broad categories of cattle: fat cattle or culls. Fat cattle are generally young (under 36 months), while cull cattle are older cows and bulls that have been culled from the herd for various reproductive or performance-related reasons.

*Revisiting Brucellosis in the Greater Yellowstone Area***TABLE 5-3** Estimated Number of Samples Collected by Slaughter Plant for FY2017 (October 1, 2016, through September 30, 2017)

Slaughter Plant by State	Estimated Number of Samples
California	180,000
Colorado (2 bison plants)	26,000
Minnesota	138,000
Nebraska	410,000
Pennsylvania	115,000
Texas (2 plants)	438,000
Utah	75,000
Wisconsin	110,000
TOTAL	1,492,000

SOURCE: Herriott, 2017.

States in which a wildlife reservoir of *B. abortus* exists are required to describe and justify the boundaries of the DSA in a USDA-APHIS approved Brucellosis Management Plan (BMP). USDA-APHIS conducted a review of the three states' BMPs for the first and only time in 2012. The reports generated from the reviews describe the strengths and weaknesses of each state's implementation of its DSA and BMP, and they provide recommendations for improvement. Collectively, the reports also reflect the wide variation in how each state sets, monitors, and enforces DSA boundaries and regulations. Variation also exists in testing requirements for movement of livestock outside the DSA, exemptions for testing, timing of testing, and how state agencies permit movement and enforce DSA-related testing (USDA-APHIS, 2012). For example, all three states require testing of sexually intact "test eligible" cattle that change ownership or are moved from the DSA within 30 days of such an event. Yet Montana and Wyoming define test eligible cattle as 12 months and older, while Idaho defines the test eligible age as 18 months and older. Montana includes bulls in its definition of test eligible animals, while Idaho and Wyoming do not. Although bulls are not thought to spread brucellosis, it is an interesting surveillance finding that only infected bulls were identified as a result of DSA-related testing in 3 of the 10 cattle and domestic bison herds designated as infected in Montana between 2007 and 2016. Also, Idaho tests only animals that reside in the DSA anytime between January 1 and June 15 of the calendar year, while Wyoming waives the 30-day requirement if the test is conducted between August 1 and January 31, and Montana considers this same exemption for cattle tested between July 16 and February 15. All three states allow movement without testing to approved livestock auction markets, provided those markets will test eligible cattle upon arrival before sale.

Idaho, Montana, and Wyoming have each expanded their DSA boundaries at least once since the initial development of those boundaries. The most common reason for DSA expansion is finding seropositive elk outside the current DSA boundaries, although there are no uniform recommendations or requirements for states to adjust DSA boundaries based on seroprevalence of *B. abortus* in wildlife. Surveillance conducted by WGFD has identified seropositive elk outside the DSA each year from 2012-2015, yet the boundaries of the DSA have not been adjusted since the last USDA review in 2012. As previously noted, culled livestock leaving this area may or may not be subject to slaughter surveillance or testing at livestock auction markets. Lack of testing adult livestock from areas where seropositive wildlife have been identified may represent an unknown risk of disease transmission. Additional standardization of DSA designations and oversight of DSA surveillance and associated movement controls by USDA-APHIS may be warranted to prevent movement of potentially infected livestock outside high-risk areas. In addition, more frequent reviews of state BMPs by USDA-APHIS may ensure that the three states are uniformly adhering to their plans in accordance with national animal health program goals.

Federal, State, and Regional Management Efforts

Seropositive elk have been found in some areas outside DSA boundaries. If adjustments are not accordingly made to the DSA boundaries in recognition of expanding seropositive wildlife, then cattle residing in those areas may not be subject to DSA testing requirements and early detection opportunities may be missed.

6. BISON SEPARATION AND QUARANTINE

Quarantining bison, followed by repeated test and removal of positive animals, is a viable tool for establishing brucellosis-free bison from infected bison populations. In December 2000, state and federal agencies involved in the management of YNP bison reached a record of decision to implement the IBMP for the purpose of managing bison that exit YNP into the state of Montana. In negotiations and hearings that were conducted to develop the IBMP, agencies were instructed to examine the feasibility of bison quarantine, with the intent of being able to certify bison as brucellosis free. There have also been frequent discussions regarding bison conservation strategies in North America and the potential for restoring the species to grassland ecosystems (Ryan Clarke et al., 2014). The agencies agreed that capturing and relocating bison to other suitable habitats would be an appropriate alternative to lethally removing bison that exceeded population objectives for YNP, as described in the IBMP. As a result, the USDA-APHIS Brucellosis Eradication Uniform Methods and Rules (UM&R) (USDA-APHIS, 2003) included a proposed quarantine protocol to ultimately qualify bison from YNP and the Grand Teton National Park as brucellosis free.

A study was conducted to determine whether the proposed UM&R protocol could be used to qualify animals originating from the YNP bison herd as free from brucellosis, including latent infections (Ryan Clarke et al., 2014). The study validated the quarantine protocol as outlined in the UM&R, and it demonstrated that it is feasible to take subadult seronegative bison from an infected bison population and qualify animals as free of brucellosis in less than 3 years (Ryan Clarke et al., 2014). Because the primary method of transmitting brucellosis in the YNP herd is through abortion and birthing events, removing bison at less than 1 year of age from the infected herd minimizes the field exposure of each animal to *B. abortus* (Ryan Clarke et al., 2014). Additional data were provided to indicate that a seropositive result is an accurate indicator of infection, supporting the approved testing protocol for older bison as outlined in the UM&R and demonstrating that collection of tissues and swab samples immediately after birth was essential to accurately determine that bison are not shedding *B. abortus* (Ryan Clarke et al., 2014). Thus, utilizing a separation and quarantine procedure to obtain brucellosis-free bison from the YNP herd provides a viable conservation measure to obtain genetically pure bison for repopulating other grassland ecosystems. While separation and quarantine could be used to safely remove bison from the YNP herd, the value of this approach for overall bison population control in YNP is limited by logistical challenges of separating and quarantining hundreds of animals annually.

7. COSTS OF PROGRAMS

Two key points underlying ongoing contention on brucellosis in the GYA are the direct monetary costs and combined benefits of brucellosis oriented programs by multiple parties operating in the GYA. Economic value estimates can vary greatly depending on the set of factors considered and the scope of the evaluation. For example, the economic value of wildlife is larger if including the entire country's demand for tourism viewing. Similarly, the economic value of disease mitigation efforts that private livestock owners may undertake is larger if the entire nation's livestock herd is considered rather than solely considering the herd residing within the GYA. No known study has comprehensively documented direct monetary costs. Similarly, the committee is unaware of any systematic assessment of associated benefits and effectiveness of how existing programs mitigate brucellosis risks. To provide context, even if not all inclusive, this section includes estimates to document substantial expense to both private and public parties and highlights the lack of a more comprehensive assessment as a critical knowledge gap.

Revisiting Brucellosis in the Greater Yellowstone Area

The national scope of bovine brucellosis concerns is clearly reflected by state, federal, and private eradication efforts exceeding \$3.5 billion over the past 75 years (NRC, 1998; Ruckelshaus Institute of Environment and Natural Resources, 2010). The GYA is estimated to support roughly 450,000 cattle and calves² that have the potential to come into contact with approximately 125,000 elk and 3,000 to 6,000 bison residing in the GYA (Schumaker et al., 2012). The populations of livestock and wildlife outside the GYA are also substantial. The magnitude of these populations is key to understanding the ongoing private and public costs of brucellosis mitigation efforts. Moreover, recognizing that DSAs in all three GYA states have expanded since 2010 reiterates the impact of these populations interacting across expanding geographic space (personal communication, D. Herriott, USDA-APHIS, 2015). The following sections provide examples of costs incurred in current mitigation efforts and programs in cattle and wildlife.

7.1 Cattle

Most livestock operations make decisions motivated by profit-oriented goals. Even though risk reduction options are available to livestock producers, those options may not appear advantageous to producers or are only partially implemented because the costs borne by individual producers outweigh the potential benefits. This reflects the reality that private costs and benefits need to be taken into account when considering policies and procedures to address brucellosis.

Ongoing livestock producer costs include expenses associated with an array of brucellosis management activities, including fencing haystacks, modifying winter feeding practices, vaccinating and spaying, and ongoing herd testing (Schumaker et al., 2012). The annual costs of ranch-level brucellosis management efforts range from \$200 to \$18,000 per operation (Roberts, 2011). Increased production costs from required brucellosis testing may range from \$1.50 to \$11.50 per head, with an estimated 330,000 cattle in Wyoming tested in 2004 alone (Bittner, 2004). Given this, in 2004 the combined testing costs to Wyoming producers were estimated to total between \$495,000 and \$3.7 million per year (Ruckelshaus Institute of Environment and Natural Resources, 2010). Those estimates do not include the expenses incurred by the owner (i.e., gathering, sorting, and handling the cattle) or the potential loss of market opportunities. Moreover, the effectiveness of these efforts in reducing risks largely remains unknown (Schumaker et al., 2012).

Separate from ongoing testing and compliance expenses, the costs of implementing brucellosis prevention activities and expenses realized under quarantines for a single producer could be considerable. Schumaker and colleagues (2012) estimate that if a 400-head cow-calf operation was quarantined during the winter feeding season following contact with an infected herd, uncompensated costs incurred by the producer would be \$2,000 to \$8,000 (Schumaker et al., 2012). If this producer's herd is positive for brucellosis, the uncompensated costs are estimated at \$35,000 to \$200,000.

Considering a representative cow/calf-long yearling operation in Wyoming, Roberts and colleagues (2012) provide estimates of annual expenses and the baseline level of risk reduction (effectiveness) needed for the operation to break even in implementing each brucellosis prevention activity (see Table 2-3 in Roberts et al., 2012). For most mitigation activities, even if mitigation resulted in complete risk reduction (e.g., 100% effectiveness), the private decision would remain to *not* adopt because implementation and maintenance costs are higher than the benefits of risk reduction (Roberts et al., 2012). This underlies the central aspects of private versus public considerations and economics of externalities.

While these estimates (Roberts et al., 2012; Schumaker et al., 2012) are valuable in understanding the economic situation faced by an individual operation, they do so in a status quo manner without consideration of broader social or whole-system effects. That is, the distinction between private break-even analyses and whole system or societal optimization is critical because individual break-even points are identified presuming no external cost-sharing or outside incentivizing of adoption. While it is critical to understand economic incentives of individual cattle producers (Pendell et al., 2010; Tonsor and Schroeder, 2015), it is also important to understand the aggregate impacts and the prospect for policies that reflect social outcomes

²Data available on livestock numbers are aggregated to the county level by USDA's National Agricultural Statistics Service to protect the confidentiality of livestock operations.

Federal, State, and Regional Management Efforts

and hence alter individual incentives to adjust their behavior. This broader aggregate understanding remains a key knowledge gap in understanding the broader impacts of brucellosis.

At the state level, the Wyoming Livestock Board incurred more than \$1 million in brucellosis expenses between July 2012 and June 2014 (personal communication, J. Logan, October 2015). While the state of Wyoming pays for required brucellosis testing of cattle, producers still incur expenses every time an animal is handled. The cost of working an animal through a chute is between \$6 and \$11 reflecting injury, equipment, labor, and animal shrink (personal communication, J. Logan, October 2015). Moreover, another expense is lost market access or price discounts by buyers of cattle originating from within DSAs (personal communication, J. Logan, October 2015). As the DSA expands, the total number of cattle suspect to these impacts grows as additional cattle operations become directly impacted.

There are a few documented cases of cow-calf operations switching to stocker operations to reduce brucellosis-related expenses. The limited number of enterprise changes largely reflects a view that such adjustments are not cost-effective or feasible given biological and market forces (personal communication, J. Logan, October 2015). This, however, reflects a situation where broader social evaluation of the optimal split between cow-calf and stocker has yet to be examined, nor has there been any consideration of policies that may encourage additional shifting away from cow-calf production.

While a large brucellosis outbreak would result in substantial economic costs, perhaps \$100-\$300 million, the small reduction in probability of an already low-frequency event make testing of all DSA-origin breeding cattle something that is not deemed a cost-effective brucellosis mitigation strategy (USDA-APHIS, 2014). These cost estimates—and hence the conclusion that testing of all DSA-origin breeding cattle is not cost-effective—may not capture all involved expenses such as the costs involved if an infected animal went initially undetected or the costs associated with risks of incubating heifers who may test negative until close to calving only to be erroneously exported from the GYA.

7.2 Wildlife

The annual expenses incurred by state and federal agencies toward elk feeding operations are worth noting. Under average conditions, the estimated annual feeding costs for the NER (7,500 elk for 79 feeding days) is \$337,488 in 1999 dollars, with alfalfa pellets being the largest expense item (Smith, 2001). This also suggests that the cost of wintering one elk is about \$56 (in 1999 dollars) per winter, with estimates ranging from \$35 to \$112. These expenses do not include fixed expenses such as administration, contracting, or monitoring of feeding programs, which likely are substantial (personal communication, E. Cole, U.S. Fish & Wildlife Service, 2015). For example, IDFG (2015) estimates that approximately \$100,000 is spent annually in Idaho's state elk brucellosis management plan, yet Idaho is home to significantly fewer elk than Wyoming.

7.3 Multi-Species, Federal Programs

Some federal program expenditures are allocated to individual states without a specific application to targeting cattle, elk, or bison. Cooperative agreements focused on brucellosis in Idaho, Montana, and Wyoming have ranged from \$1.26 million to \$1.72 million per year over the past 6 years (personal communication, D. Herriott, USDA-APHIS, 2015). These federal funds are used to cover expenses of maintaining DSAs in the three GYA states. More broadly, a very small portion of federal program expenditures are allocated to research, and most is spent focused on testing and surveillance. While the Agricultural Act of 2014 (better known as the 2014 Farm Bill) did authorize brucellosis as a priority area for research due to its classification as a zoonotic disease with a wildlife reservoir, funds have yet to be appropriated for this priority issue to date.

Revisiting Brucellosis in the Greater Yellowstone Area

REFERENCES

- Belfrage, J. 2015. National brucellosis program update. Pp. 165-166. Proceedings One Hundred and Eighteenth Annual Meeting of the U.S. Animal Health Association, October 16-22, 2014, Kansas City, MO. Available online at <http://www.usaha.org/Portals/6/Proceedings/2014%20USAHA%20Proceedings%20web.pdf> (accessed January 6, 2017).
- Bittner, A. 2004 An Overview and the Economic Impacts Associated with Mandatory Brucellosis Testing in Wyoming Cattle. Wyoming Department of Administration and Information. Available online at http://eadmin.state.wy.us/specialreports/Brucellosis_report.pdf (accessed January 6, 2017).
- BLM (Bureau of Land Management). 2016. Fact Sheet on BLM's Management of Livestock Grazing. U.S. Department of the Interior, Bureau of Land Management. Available online at <http://www.blm.gov/wo/st/en/prog/grazing.html> (accessed June 4, 2016).
- Brunner, R.D., C.H. Colburn, C.M. Cromley, R. A. Klein, and E.A. Olson. 2002. Finding Common Ground: Governance and Natural Resources in the American West. New Haven, CT: Yale University Press.
- Carter, M. 2012. Moving forward with the brucellosis eradication program. Pp. 180-182 in Proceedings One Hundred and Fifteenth Annual Meeting of the U.S. Animal Health Association, September 29-October 5, 2011, Buffalo, NY. Available online at <http://www.usaha.org/Portals/6/Proceedings/USAHAProceedings-2011-115th.pdf> (accessed January 6, 2017).
- Carter, M. 2013. National brucellosis program update. Pp. 196-198 in Proceedings One Hundred and Sixteenth Annual Meeting of the U.S. Animal Health Association, October 18-24, 2012, Greensboro, NC. Available online at <http://www.usaha.org/Portals/6/Proceedings/USAHAProceedings-2012-116th.pdf> (accessed January 6, 2017).
- Creech, T., P.C. Cross, B.M. Scurlock, E.J. Maichak, J.D. Rogerson, J.C. Henningsen, and S. Creel. 2012. Effects of low-density feeding on elk-fetus contact rates on Wyoming feedgrounds. *Journal of Wildlife Management* 76(5):877-886.
- Enright, F.M. 1990. The pathogenesis and pathobiology of *Brucella* infection in domestic animals. Pp. 301-320 in *Animal Brucellosis*. K. Nielsen, and J.R. Duncan, eds. Boca Raton, FL: CRC Press.
- FWS (U.S. Fish & Wildlife Service). 2016a. FWS Fundamentals. Available online at <http://www.fws.gov/info/pocketguide/fundamentals.html> (accessed January 30, 2016).
- FWS. 2016b. National Elk Refuge: About the Refuge. Available online at https://www.fws.gov/refuge/National_Elk_Refuge/about.html (accessed January 30, 2016).
- FWS. 2016c. National Elk Refuge: Elk. Available online at <http://www.fws.gov/nwrs/threecolumn.aspx?id=2147515027> (accessed January 30, 2016).
- FWS. 2016d. National Elk Refuge: Bison. Available online at <http://www.fws.gov/nwrs/threecolumn.aspx?id=2147515045> (accessed January 30, 2016).
- Galey, F. 2015. Efforts by the Wyoming Brucellosis Coordination Team and the Consortium for the Advancement of Brucellosis Science. Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 16, 2015, Jackson Lake Lodge, WY.
- Glynn, M.K., and T.V. Lynn. 2008. Zoonosis update: Brucellosis. *Journal of the American Veterinary Medical Association* 233(6):900-908.
- GYIBC (Greater Yellowstone Interagency Brucellosis Committee). 2005. GYIBC Annual Report. Available online at <https://archive.org/details/gyibcannualrepor2005grea> (accessed March 25, 2016).
- Herriges, J.D., E.T. Thirne, S.L. Anderson, and H.A. Dawson. 1989. Vaccination of elk in Wyoming with reduced dose strain 19 *Brucella*: Controlled studies and ballistic implant field trials. *Proceedings of the U.S. Animal Health Association* 93:640-655.
- Herriott, D. 2017. Updated information based on Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Jackson Lake Lodge, WY.
- IBMP (Interagency Bison Management Plan). 2016. Interagency Bison Management Plan. Available online at <http://www.ibmp.info> (accessed March 25, 2016).
- IDFG (Idaho Department of Fish and Game). 2015. Idaho Fish and Game 2015 Strategic Plan. Available online at <http://fishandgame.idaho.gov/public/about/?getPage=191> (accessed March 22, 2016).
- IDFG. 2016. Fish and Game Mission Statement. Available online at <http://fishandgame.idaho.gov/public/about/commission/?getPage=186> (accessed March 22, 2016).
- Maichak, E.J., B.M. Scurlock, J.D. Rogerson, L.L. Meadows, A.E. Barbknecht, W.H. Edwards, and P.C. Cross. 2009. Effects of management, behavior, and scavenging on risk of brucellosis transmission in elk of western Wyoming. *Journal of Wildlife Diseases* 45(2):398-410.

Federal, State, and Regional Management Efforts

- Maichak, E.J., B.M. Scurlock, P.C. Cross, J.D. Rogerson, W.H. Edwards, B. Wise, S.G. Smith, and T.J. Kreeger. 2017. Assessment of a strain 19 brucellosis vaccination program in elk. *Wildlife Society Bulletin* 41:70-79.
- MFWP (Montana Fish, Wildlife & Parks). 2016a. Montana Fish Wildlife and Parks: About Us. Available online at <http://fwp.mt.gov/doingBusiness/insideFwp/aboutUs.html> (accessed March 22, 2016).
- MFWP. 2016b. Montana Statewide Elk Management. Available online at <http://fwp.mt.gov/fishAndWildlife/management/elk> (accessed March 23, 2016).
- NPS (National Park Service). 2016a. National Park Service: What We Do. Available online at <http://www.nps.gov/aboutus/index.htm> (accessed January 30, 2016).
- NPS. 2016b. Yellowstone Center for Resources: Annual Reports—Yellowstone National Park. Available online at https://www.nps.gov/yell/learn/management/ycrannual_report.htm (accessed March 25, 2016).
- NRC (National Research Council). 1998. *Brucellosis in the Greater Yellowstone Area*. Washington, DC: National Academy Press.
- OMB (Office of Management and Budget). 2007. Report to Congress on the Costs and Benefits of Regulations and Unfunded Mandates on State, Local, and Tribal Entities. Available online at https://www.whitehouse.gov/omb/inforeg_regpol_reports_congress (accessed January 30, 2016).
- Pendell, D.L., G.W. Brester, T.C. Schroeder, K.C. Dhuyvetter, and G.T. Tonsor. 2010. Animal identification and tracing in the United States. *American Journal of Agricultural Economics* 92(4):927-940.
- Plumb, G., L. Babiuk, J. Mazet, S. Olsen, P.P. Pastoret, C. Rupprecht, and D. Slate. 2007. Vaccination in conservation medicine. *Revue scientifique et technique (International Office of Epizootics)* 26(1):229-241.
- Ragan, V.E. 2002. The Animal and Plant Health Inspection Service (APHIS) brucellosis eradication program in the United States. *Veterinary Microbiology* 90(1-4):11-18.
- Rhyan, J.C., P. Nol, C. Quance, A. Gertonson, J. Belfrage, L. Harris, K. Straka, and S. Robbe-Austerman. 2013. Transmission of brucellosis from elk to cattle and bison, Greater Yellowstone area, U.S.A., 2002-2012. *Emerging Infectious Diseases* 19(12):1992-1995.
- Roberts, T.W. 2011. Costs and Expected Benefits to Cattle Producers of Brucellosis Management Strategies in the Greater Yellowstone Area of Wyoming. M.S. Thesis, Department of Agricultural and Applied Economics, University of Wyoming, Laramie, WY.
- Roberts, T.W., D.E. Peck, and J.P. Ritten. 2012. Cattle producers' economic incentives for preventing bovine brucellosis under uncertainty. *Preventive Veterinary Medicine* 107(3-4):187-203.
- Roffe, T.J., L.C. Jones, K. Coffin, M.L. Drew, S.J. Sweeney, S.D. Hagius, P.H. Elzer, and D. Davis. 2004. Efficacy of single calfhood vaccination of elk with *Brucella abortus* strain 19. *Journal of Wildlife Management* 68(4):830-836.
- Ruckelshaus Institute of Environment and Natural Resources. 2010. Fact Sheet on the Consortium for the Advancement of Brucellosis Science (CABS): A Scientific Synthesis to Inform Policy and Research, January 2010. Available online at [http://www.emwh.org/issues/brucellosis/CABS/2010-revised-cabs-fact-sheet\(1\).pdf](http://www.emwh.org/issues/brucellosis/CABS/2010-revised-cabs-fact-sheet(1).pdf) (accessed January 6, 2017).
- Ryan Clarke, P., R.K. Frey, J.C. Rhyan, M.P. McCollum, P. Nol, and K. Aune. 2014. Feasibility of quarantine procedures for bison (*Bison bison*) calves from Yellowstone National Park for conservation of brucellosis-free bison. *Journal of American Veterinary Medical Association* 244(5):588-591.
- Schumaker, B.A., D.E. Peck, and M.E. Kauffman. 2012. Brucellosis in the Greater Yellowstone area: Disease management at the wildlife—livestock interface. *Human—Wildlife Interactions* 6(1):48-63.
- Scurlock, B.M. 2015. Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Jackson Lake Lodge, WY.
- Scurlock, B.M., W.H. Edwards, T. Cornish, and L. Meadows. 2010. Using Test and Slaughter to Reduce Prevalence of Elk Attending Feedgrounds in the Pinedale Elk Herd Unit of Wyoming: Results of a 5-year Pilot Project. Available online at https://wgfd.wyo.gov/WGFD/media/content/PDF/Wildlife/TR_REPORT_2010_FINAL.pdf (accessed June 4, 2016).
- Slate, D., T.P. Algeo, K.M. Nelson, R.B. Chipman, D. Donovan, J.D. Blanton, M. Niezgod, and C.E. Rupprecht. 2009. Oral rabies vaccination in North America: Opportunities, complexities, and challenges. *PLOS Neglected Tropical Diseases* 3(12):e549.
- Smith, B.L. 2001. Winter feeding of elk in western North America. *Journal of Wildlife Management* 65(2):173-190.
- Thorne, E.T., T.J. Kreeger, T.J. Walthall, and H.A. Dawson. 1981. Vaccination of elk with strain 19 *Brucella abortus*. *Proceedings of the U.S. Animal Health Association* 85:359-374.
- Tonsor, G.T., and T.C. Schroeder. 2015. Market impacts of *E. Coli* vaccination in U.S. Feedlot cattle. *Agricultural and Food Economics* 3:7.

Revisiting Brucellosis in the Greater Yellowstone Area

- U.S. Congress. 2007. Oversight Hearing Before the Subcommittee on National Parks, Forests, and Public Lands of the Committee on Natural Resources, U.S. House of Representatives. Serial No. 110-7. March 20. Available online at <https://www.gpo.gov/fdsys/pkg/CHRG-110hrg34137/html/CHRG-110hrg34137.htm> (accessed March 25, 2016).
- USAHA (U.S. Animal Health Association). 2001. Pp. 122-123 in USAHA Proceedings from the One Hundred and Fifth Annual Meeting, November 1-8, 2001. Pat Campbell and Associates, Richmond, VA, and Thomson-Shore, Inc., Dexter, MI.
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2003. Brucellosis Eradication: Uniform Methods and Rules. APHIS 91-45-013. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/umr_bovine_bruc.pdf (accessed June 4, 2016).
- USDA-APHIS. 2009. A Concept Paper for a New Direction for the Bovine Brucellosis Program. Available online at https://www.avma.org/sites/default/files/resources/0912_concept_paper_for_bovine_br_program_aphis-2009-0006-0002.pdf (accessed June 4, 2016).
- USDA-APHIS. 2010. National Brucellosis Surveillance Strategy, December, 2010. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/natl_bruc_surv_strategy.pdf (accessed June 4, 2016).
- USDA-APHIS. 2012. Review of Montana's Brucellosis Management Plan. Available online at https://liv.mt.gov/Portals/146/brucellosis/DSA/2012_MT_DSA_REVIEW.pdf (accessed November 16, 2020).
- USDA-APHIS. 2014. Brucellosis Regionalization Risk Assessment Model: An Epidemiologic Model to Evaluate the Risk of *B. abortus* Infected Undetected Breeding Cattle Moving out of the Designated Surveillance Areas in Idaho, Montana, and Wyoming. Fort Collins, CO: Center for Epidemiology and Animal Health. December 2014. 54 pp.
- USDA-APHIS. 2015. About APHIS. Available online at <https://www.aphis.usda.gov/aphis/banner/aboutaphis> (accessed January 30, 2016).
- USDO/USDA (U.S. Department of the Interior and U.S. Department of Agriculture). 2000. Record of Decision for Final Environmental Impact Statement and Bison Management Plan for the State of Montana and Yellowstone National Park, December 20, 2000. U.S. Department of the Interior, National Park Service, and U.S. Department of Agriculture, U.S. Forest Service, Animal and Plant Health Inspection Service. Available online at <https://www.nps.gov/yell/learn/management/upload/yellbisonrod.pdf> (accessed January 4, 2017).
- USFS (U.S. Forest Service). 2016. U.S. Forest Service: About the Agency. Available online at <http://www.fs.fed.us/about-agency> (accessed January 30, 2016).
- WBCT (Wyoming Brucellosis Coordination Team). 2005. Wyoming Brucellosis Coordination Team Report & Recommendations. January 11. Available online at http://www.wyomingbrucellosis.com/_pdfs/brucellosisCoordReport.pdf (accessed June 14, 2016).
- WGFD (Wyoming Game & Fish Department). 2016a. About the Wyoming Game and Fish Department. Available online at <https://wgfd.wyo.gov/About-Us/About-the-Department> (accessed March 22, 2016).
- WGFD. 2016b. Brucellosis Reports: Brucellosis Management Action Plans. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed March 23, 2016).
- Wyoming Livestock Board. 2016. Wyoming Livestock Board: Animal Health. Available online at <https://wsb.state.wy.us/public/animal-health> (accessed March 22, 2016).

6

Adaptive Management

The concept of adaptive management has existed for decades (Holling, 1978; Walters, 1986; Reeve Morghan et al., 2006, McCarthy and Possingham, 2007; Williams et al., 2009, Williams, 2011; Allen et al., 2013; Allen and Garmestani, 2015). As indicated in the previous National Research Council (NRC) (1998) report, “an adaptive management approach that has research designed to provide data to reduce areas of current uncertainty should eventually give a more realistic assessment of the feasibility of eradication of *B. abortus* in the GYA [Greater Yellowstone Area].” Although resource managers are generally aware of the approach, the term continues to be misused and misunderstood (Williams, 2011). In addressing brucellosis, the term “adaptive management” is used in different ways and its meaning has not always been clear. In this chapter, the committee reexamines adaptive management in the context of addressing brucellosis in the GYA and offers clarification for correction.

1. DEFINING ADAPTIVE MANAGEMENT

Adaptive management is most clearly and succinctly defined as “a systematic approach for improving resource management by learning from management outcomes” (Williams et al., 2009). Adaptive management is a form of structured decision making that is carried out iteratively over time, as opposed to a process that is applied only once (Martin et al., 2009). Structured decision making enables decision makers to focus on what, why, and how actions will be taken. It involves stakeholder engagement, problem identification, specification of objectives, identifying alternative approaches, projecting the consequences, and identifying uncertainties (Williams et al., 2009). The following definition of adaptive management is cited by the U.S. Department of the Interior’s (DOI’s) technical guide (Williams et al., 2009) and adopted from the 2004 NRC report *Adaptive Management for Water Resources Project Planning*:

Adaptive management [is a decision process that] promotes flexible decision making that can be adjusted in the face of uncertainties as outcomes from management actions and other events become better understood. Careful monitoring of these outcomes both advances scientific understanding and helps adjust policies or operations as part of an iterative learning process. Adaptive management also recognizes the importance of natural variability in contributing to ecological resilience and productivity. It is not a “trial and error” process, but rather emphasizes learning while doing. Adaptive management does not represent an end in itself, but rather a means to more effective decisions and enhanced benefits. Its true measure is in how well it helps meet environmental, social, and economic goals, increases scientific knowledge, and reduces tensions among stakeholders. (NRC, 2004)

According to the original authors of the concept (Walters and Holling, 1990), there are three ways to structure management as an adaptive process (Walters, 1986): (1) evolutionary, or “trial and error,” in which early choices are essentially haphazard, while later choices are made from a subset that gives better results; (2) passive adaptive, where historical data available at each time are used to construct a single best estimate or model for response, and the decision choice is based on assuming this model is correct; or (3) active adaptive, where data available at each time are used to structure a range of alternative response

Revisiting Brucellosis in the Greater Yellowstone Area

models, and a policy choice is made that reflects some computed balance between expected short-term performance and long-term value of knowing which alternative model (if any) is correct. Active adaptive management seeks to increase the rate of learning by applying two or more management actions simultaneously, which are in turn based on alternate hypotheses or models of system function. When it is possible to carry out an active approach, it is possible to decide which experimental approaches should be optimally tested based on what is already known about the likelihoods of system responses and associated risks (Walters and Holling, 1990). As in any scientific experimentation, it is necessary to pay attention to principles of statistical design such as controls, randomization, replication, and stratification.

Williams and colleagues (2009) put forth six steps of adaptive management: (1) assessing the problem; (2) designing a management approach; (3) implementing the management approach; (4) monitoring the responses to the management actions; (5) evaluating the responses; and (6) adjusting the management approach based on what was learned (Williams et al., 2009). These six steps are then repeated over time. Westgate and colleagues (2013) outlined an alternative set of six steps: (1) identification of management goals in collaboration with stakeholders; (2) specification of multiple management options, one of which can be “do nothing;” (3) creation of a rigorous statistical process for interpreting how the system responds to management interventions, which typically involves creation of quantitative models and/or a rigorous experimental design; (4) implementation of management action(s); (5) monitoring of system response to management interventions (preferably on a regular basis); and (6) adjust management practice in response to results from monitoring (Westgate et al., 2013). Step 3 from the latter is key to active adaptive management. It is essentially equivalent to the scientific method of hypothesis formulation (conceptual modeling) and hypothesis testing (using well-formulated experimental designs). Experimentation is used not only to support or refute hypotheses but also to provide new knowledge that can be used to incrementally refine or replace the hypotheses and the model.

Modeling is essential to the process of adaptive management, as models provide the basis for making predictions of how the system will respond to management actions as well as other environmental variations. A model, its structure, and its parameters embody a set of hypotheses about how the system works. A model can be conceptual or quantitative, but it always embodies current understanding and can be used to make informed predictions of system dynamics in response to the environment or management actions. Model predictions are compared with data, and the hypothesis is then rejected, supported, or revised.

Modeling has often been beneficially used to inform bison and elk management in the GYA. For example, models have been built of bison movements (Bruggeman et al., 2007; Geremia et al., 2011, 2014a), bison population dynamics (Coughenour, 2005; Geremia et al., 2011, 2014b; Hobbs et al., 2015), elk population dynamics (Coughenour and Singer, 1996; Taper and Gogan, 2002; Lubow and Smith, 2004; Eberhart et al., 2007), elk-wolf dynamics (Varley and Boyce, 2006), elk spatial distributions (Mao et al., 2005; Cross et al., 2010b), brucellosis transmission and seroprevalence (Cross et al., 2010a; Hobbs et al., 2015), and ecosystem dynamics (Coughenour, 2002, 2005). These models simulate and predict system responses to various management actions, and researchers and resource managers use the models’ insights and predictions to make informed management decisions.

New modeling approaches have recently been used to incorporate epidemiological, demographic, and ecological processes across space and time. These include improved epidemiological models, spatially explicit population models, Bayesian models, ecosystem models, and linked epidemiological-demographic models (Cross et al., 2010a; Hobbs et al., 2015). Spatial modeling has advanced markedly in the last two decades, and spatial heterogeneity and processes have increasingly been recognized as critical for understanding wildlife ecology and ecosystem dynamics. Land use change and its drivers have also been modeled with increasingly sophisticated approaches over the past two decades (e.g., Agarwal et al., 2002; Basse et al., 2014). Such landscape models could be useful in addressing brucellosis, as these models can incorporate animal disease dynamics and the effects of land use and wildlife management across spatially heterogeneous ecosystems (Millsbaugh et al., 2008; Sandifer et al., 2015).

Adaptive Management

Models also address uncertainty, another hallmark of adaptive management. It is essential to explicitly acknowledge uncertainties arising in model formulation, parameterization, and environmental variability. Once the sources of uncertainty are quantitatively identified, experiments can be designed to reduce uncertainties in parameter estimation and more attention can be given to key aspects of model formulation. Uncertainty can be stated qualitatively or quantitatively. There are a number of different ways to quantify uncertainty, including simple statistics, information theoretic statistics, uncertainty analysis, sensitivity analysis, model verification, and validation. Bayesian statistics was suggested early on to be particularly well suited for adaptive management (Walters, 1986), and this approach has been useful in modeling the best options for managing brucellosis in GYA bison (Hobbs et al., 2015).

Adaptive management plans for bison, elk, and brucellosis in the Greater Yellowstone Ecosystem (GYE) could make greater uses of models in identifying and evaluating management actions. Models serve as formal hypotheses of the ways that populations, disease, and ecosystems function and respond to management actions. Models could also be used to a greater extent as focal points for multi-stakeholder involvement and understanding.

2. ADAPTIVE MANAGEMENT IN THE GREATER YELLOWSTONE AREA: CASE STUDIES

2.1 The Interagency Bison Management Plan

Adaptive management is employed with the Interagency Bison Management Plan (IBMP) and the U.S. Fish & Wildlife Service (USFWS) management plan for elk in the southern GYE (USDOI and USDA, 2000a,b; USFWS and NPS, 2007), but there are areas for improvement. The IBMP calls for an adaptive management program that “includes intensive monitoring and coordination, as well as research projects with specified resultant management actions responding to the research results” (USDOI and USDA, 2000b). This was also specified in the modified preferred alternative in the Environmental Impact Statement (USDOI and USDA, 2000a):

In the context of the bison management plan and the modified preferred alternative, adaptive management means testing and validating with generally accepted scientific and management principles the proposed spatial and temporal separation risk management and other management actions. Under the adaptive management approach, future management actions could be adjusted, based on feedback from implementation of the proposed risk management actions.... By its nature, a plan using adaptive management requires monitoring and adjustments as new information is obtained.

Response to 2008 GAO Report

In 2008, the U.S. Government Accountability Office (GAO) issued a review that was critical of the IBMP’s implementation and pointed out essential components of adaptive management that were lacking (GAO, 2008). According to the GAO, the implementation of the IBMP lacked: (1) linkages among key steps, including identifying measurable management objectives, a monitoring program about the impacts of management actions, and decision making based on lessons learned from past management actions; (2) key agency partner collaborations; and (3) engagement of key stakeholders (GAO, 2008). In response, agencies involved in implementing the IBMP made significant improvements in their approach. Adjustments to the IBMP were based on the adaptive management framework and principles outlined in the DOI’s technical guide on adaptive management (Williams et al., 2009). Beginning in 2008, the IBMP has produced annual report updates describing adaptive adjustments to the IBMP, and these reports are posted online. In particular, the adjustments to the IBMP included the creation of measurable objectives and the development of a specific monitoring program to assess important scientific and management questions (IBMP, 2008).

Revisiting Brucellosis in the Greater Yellowstone Area

The IBMP annual adaptive management reports are highly structured and are based on principles of structured decision making with stated overarching goals and a series of management objectives. For each objective, a series of management actions are described; and for each action, a set of corresponding monitoring metrics and management responses are outlined. This framework ensures that the objectives are clearly defined and that there are clear linkages between the objectives and the other components of the IBMP. The approach can be illustrated using the example of Goal #2 from their 2014 report, with the IBMP specifying other actions aimed at increasing the understanding of bison genetics and the ecological role of bison to inform adaptive management (IBMP, 2014).

Goal #2: Conserve a wild, free-ranging bison population.

Objective 2.1. Manage the Yellowstone bison population to ensure the ecological function and role of bison in the Yellowstone area and to maintain genetic diversity for future adaptation.

Management action 2.1.a. Increase the understanding of bison population dynamics to inform adaptive management and reduce sharp increases and decreased in bison abundance.

Monitoring metric: Conduct aerial and ground surveys to estimate the annual abundance of Yellowstone bison each summer.

Management response: If abundance estimates decrease to <2,300 bison, then the agencies will increase the implementation of non-lethal management measures.

The structure of this framework appropriately links management actions to management objectives, specifies monitoring metrics to measure the responses to the actions, and specifies management responses to monitoring results. The annual reports are available online, with opportunity for public feedback. The approach has proven to be successful because the goals and objectives are agreed on by the IBMP agencies and because the proposed management actions are based on practical knowledge, experience, scientific research, and creative thought. Importantly, the objectives are stated and results of management actions taken to achieve the objective are monitored and reported. This provides the transparency and accountability that the GAO had previously noted was needed (GAO, 2008).

Need for Clarification Due to Varied Usage and Application

The term “adaptive management” is used in three different ways in the IBMP. The most pervasive use of the term is in reference to “adaptive management changes,” such as incrementally expanding the zone of tolerance for bison outside of Yellowstone National Park (YNP) or allowing limited hunting. Incremental changes are predicated on what has been learned through management about actions that are successful, and the assumption is that more learning will occur through applying the adaptive changes. However, there is no stated intention for carrying out adaptive management for the purpose of learning more about the system in a scientific sense.

A second way the term is used is by inference: because management actions are part of a larger adaptive management plan, these actions are considered as adaptive management actions. However, many of the stated IBMP management actions are merely statements of actions to be taken, without any apparent use of prior knowledge or intent to gain knowledge through the action. The following examples are excerpted from the IBMP (2012, 2014):

- *Management Action 1.1a: Allow untested female/mixed groups of bison to migrate onto and occupy the Horse Butte peninsula and the Flats each winter and spring in Zone 2.*
- *Management Action 1.3c: Annually, the Gallatin National Forest will ensure conflict-free habitat is available for bison and livestock grazing on public lands, as per management objectives of the IBMP.*

Adaptive Management

- *Management Action 2.2a: Use slaughter only when necessary; attempt to use other risk management tools first.*
- *Management Action 3.1a: Continue bison vaccination under prevailing authority.*

These actions would be considered passive, not active, adaptive management, as the focus is on achieving management objectives and learning becomes an untargeted byproduct (Williams et al., 2009). Some of these actions are also examples of “management based on resource status,” which is also not adaptive management (Williams et al., 2009).

The third way the term is used is more aligned with the original definition: to make decisions based on what has been learned and to carry out research to inform management. Several management actions explicitly call for knowledge and research to inform adaptive management. The following examples are drawn from the IBMP (2012, 2014):

- *Management Action 1.1b: Use adaptive management to gain management experience regarding how bison use Zone 2 in the Gardiner basin, and provide space/habitat for bison in cattle-free areas.*
- *Management Action 1.1c: Use research findings on bison birth synchrony and fetal and shed *Brucella abortus* field viability and persistence to inform adaptive management.*
- *Management Action 2.1a: Increase the understanding of bison population dynamics to inform adaptive management and reduce sharp increases and decreases in bison abundance.*
- *Management Action 2.1b: Increase the understanding of genetics of bison in YELL to inform adaptive management.*
- *Management Action 2.1c: Increase understanding of the ecological role of bison to inform adaptive management by commissioning a comprehensive review and assessment.*

However, with the possible exception of action 1.1b, the actions listed do not use management by experiment. As stated in the previous NRC report, adaptive management has “research designed to provide data to reduce areas of current uncertainty,” and it means “conducting management activities as hypothesis tests.” This corresponds to active adaptive management, which uses experimental management that focuses directly on learning, or “quasi-experimental management that focuses simultaneously on learning and achievement of management objectives” (Williams et al., 2009). Both approaches carry out management in ways that aim to increase learning about processes that control system dynamics, and they both involve “management by experiment.” While the other actions aim to use research findings to inform management decisions, they do not use management to learn and therefore cannot be considered as adaptive management. Whether passive or active, the hallmark of adaptive management is the intent to use management to learn about the system in order to inform future management.

2.2 Vaccination of Feedground Elk

The vaccination of feedground elk populations is an example of adaptive management applied to reducing brucellosis. At the time of the previous NRC review (1998), there was recognition that better vaccines were needed. It was known at the time that syringe vaccination was deemed inappropriate and cost-ineffective, but the lyophilization of *B. abortus* strain 19 (S19) vaccine and its incorporation into hydroxypropyl cellulose biobullets allowed remote vaccination where dense populations of elk could be closely approached on feedgrounds in winter (NRC, 1998). Thus, with the relatively new approach for vaccinating elk with S19, it was an available adaptive management tool that could be used in the short term and its successes and failures could be monitored (Thorne et al., 1981).

From the outset, success and failure was measured by trends in seroprevalence and, in some places and some years, by close observation of rates of abortion (Herriges, 1989). S19 biobullet vaccination was implemented as the primary short-term adaptive management tool for reducing brucellosis in feedground

Revisiting Brucellosis in the Greater Yellowstone Area

elk in the mid-1980s, with the hope it would reduce disease prevalence in elk and thus reduce risk of cattle exposure. At the time of the previous NRC review, declining seroprevalence suggested it might indeed be a key to reducing rates of infection in feedground elk.

Biobullet vaccination of elk with S19 continued to be monitored for 30 years, making it now one of the longest-lasting examples of adaptive management of a wildlife disease. Seroprevalence rates initially declined (Herriges et al., 1989), but long-term studies over the last decade have shown increasing seroprevalence and no decline over three decades (Schumaker, 2015; Maichak et al., 2017). *B. abortus* challenge trials revealed single calfhood vaccination with S19 had low efficacy in preventing infection; would likely have only little-to-moderate effect on *Brucella* prevalence in elk; and was unlikely to eradicate the disease in wildlife of the GYA (Roffe et al., 2004). Immunology studies revealed that vaccination of elk with S19 and *B. abortus* strain RB51 induces poor protection against brucellosis (Olsen et al., 2006). Kauffman and colleagues (2013) note that “Since 1985, nearly 100,000 elk have been inoculated. However, efficacy of S19 in preventing abortions in elk is low (25%) (Roffe et al., 2004), and reductions in brucellosis prevalence among elk attending vaccinated feed-grounds have not been observed.” Furthermore, in addition to the weight of scientific evidence against S19 vaccination of elk, it appears that the Wyoming Game & Fish Department is halting the vaccination program due to logistical constraints associated with the manufacturer discontinuing production of biobullets (Scurlock, 2015).

What started as a short-term adaptive management effort became a long-term effort and, effectively, a long-term experiment. By making adjustments along the way based on continued observation and data collection, the experiment has provided useful information on efficacy and cost-effectiveness (Maichak et al., 2017). However, a number of aspects could have led to a faster learning process and more rapid management changes. First, replicate control feedgrounds could have been used during the initiation of the program. Second, more continuous assessment of the program’s efficacy and scientific peer-review could have been conducted periodically through the process. Third, the cessation of vaccination on feedgrounds could have been implemented across different groups of feedgrounds in different years so as to control for other temporal changes.

This example shows how long-term commitment to adaptive management can reveal strengths and limitations of the applications of a particular tool or manipulation that intuitively seem likely to work. Although long-term collection of data incurs labor and analysis costs, the results can be used to inform potential decisions regarding application of S19 biobullet vaccination not only for feedground elk but also for free-ranging elk without risks and expenditures inherent in such an effort (Kauffman et al., 2013).

Other short-term (but available) adaptive management tools to reduce brucellosis infection in cattle—such as phasing out or eliminating some feedgrounds, using targeted elk population reductions, reducing spatial and temporal overlap of elk and cattle on ranges, applying physical barriers around feed—are now being tested and learning will take place through monitoring. To the extent they are efficacious and cost-effective, they may become longer-term tools or manipulations until a better option becomes feasible.

REFERENCES

- Agarwal, C., G.M. Green, J.M. Grove, T.P. Evans, and C.M. Schweik. 2002. A Review and Assessment of Land-use Change Models: Dynamics of Space, Time, and Human Choice. General Technical Report NE-297. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northeastern Research Station. 61 pp.
- Allen, C.R., and A.S. Garmestani, eds. 2015. Adaptive Management of Social-ecological Systems. Dordrecht, The Netherlands: Springer. 264 pp.
- Allen, C.R., J.J. Fontaine, and A.S. Garmestani. 2013. Ecosystems, Adaptive Management. Nebraska Cooperative Fish & Wildlife Research Unit—Staff Publications. Paper 128. University of Nebraska, Lincoln. Available online at <http://digitalcommons.unl.edu/ncfwrustaff/128> (accessed January 9, 2017).
- Basse, R.M., H. Omrani, O. Charif, P. Gerber, and K. Bodis. 2014. Land use changes modelling using advanced methods: Cellular automata and artificial neural networks. The spatial and explicit representation of land cover dynamics at the cross-border region scale. *Applied Geography* 53:160-171.

Adaptive Management

- Bruggeman, J.E., R.A. Garrott, P.J. White, F.G.R. Watson, and R. Wallen. 2007. Covariates affecting spatial variability in bison travel behavior in Yellowstone National Park. *Ecological Applications* 17:1411-1423.
- Coughenour, M.B. 2002. Executive summary of model-based assessment of elk in the Rocky Mountain National Park ecosystem. In F. J. Singer, ed. *Ecological evaluation of the abundance and effects of elk in Rocky Mountain National Park, Colorado, 1994-1999*. USGS Open File Report 02-208.
- Coughenour, M.B. 2005. Spatial-dynamic Modeling of Bison Carrying Capacity in the Greater Yellowstone Ecosystem: A Synthesis of Bison Movements, Population Dynamics, and Interactions with Vegetation. Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO.
- Coughenour, M.B., and F.J. Singer. 1996. Yellowstone elk population responses to fire: A comparison of landscape carrying capacity and spatial-dynamic ecosystem modeling approaches. Pp. 169-180 in *The Ecological Implications of Fire in Greater Yellowstone*. J. Greenlee, ed. Fairfield, WA: International Association of Wildland Fire.
- Cross, P.C., D.M. Heisey, B.M. Scurlock, W.H. Edwards, M.R. Ebinger, and A. Brennan. 2010a. Mapping brucellosis increases relative to elk density using hierarchical Bayesian models. *PLOS ONE* 5:e10322.
- Cross, P.C., E.K. Cole, A.P. Dobson, W.H. Edwards, K.L. Hamlin, G. Luikart, A.D. Middletown, B.M. Scurlock, and P.J. White. 2010b. Probable causes of increasing brucellosis in free-ranging elk of the greater Yellowstone ecosystem. *Ecological Applications* 20:278-288.
- Eberhart, L.L., P.J. White, R.A. Garrott, and D.B. Houston. 2007. A seventy-year history of trends in Yellowstone's northern elk herd. *Journal of Wildlife Management* 71:594-602.
- GAO (U.S. Government Accountability Office). 2008. *Yellowstone Bison: Interagency Plan and Agencies' Management Need Improvement to Better Address Bison-Cattle Brucellosis Controversy*. Available online at <http://www.gao.gov/new.items/d08291.pdf> (accessed January 10, 2017).
- Geremia, C., P.J. White, R.L. Wallen, F.G.R. Watson, J.J.J. Treanor, J. Borkowski, C.S. Potter, and R.L. Crabtree. 2011. Predicting bison migration out of Yellowstone National Park using Bayesian models. *PLOS ONE* 6(2):e16848.
- Geremia, C., R. Wallen, and P. J. White. 2014a. Population Dynamics and Adaptive Management of Yellowstone Bison, August 5, 2014. National Park Service, Yellowstone National Park, Mammoth, Wyoming. Available online at [http://www.ibmp.info/Library/20140730/Bison%20Population%20and%20Disease%20Model%20v6%20\(final%20for%202014\).pdf](http://www.ibmp.info/Library/20140730/Bison%20Population%20and%20Disease%20Model%20v6%20(final%20for%202014).pdf) (accessed May 25, 2017).
- Geremia, C., R. Wallen, and P. J. White. 2014b. Spatial Distribution of Yellowstone Bison-Winter 2015. National Park Service, Yellowstone National Park, Mammoth, WY. September 2014. Available online at http://www.ibmp.info/Library/OpsPlans/BisonSpatialDistributions_Final_Winter2015.pdf (accessed May 25, 2017).
- Herriges, J.D., E.T. Thirne, S.L. Anderson, and H.A. Dawson. 1989. Vaccination of elk in Wyoming with reduced dose strain 19 *Brucella*: Controlled studies and ballistic implant field trials. *Proceedings of the U.S. Animal Health Association* 93:640-655.
- Hobbs, N.T., C. Geremia, J. Treanor, R. Wallen, P.H. White, M.B. Hooten, and J.C. Rhyen. 2015. State-space modeling to support management of brucellosis in the Yellowstone bison population. *Ecological Monographs* 85(4):525-546.
- Holling, C.S., editor. 1978. *Adaptive Environmental Assessment and Management*. Chichester, UK: John Wiley & Sons.
- IBMP (Interagency Bison Management Plan). 2008. 2008 IBMP Adaptive Management Plan. National Park Service, USDA-Forest Service, USDA-Animal & Plant Health Inspection Service, Montana Department of Livestock and Montana Fish Wildlife & Parks. Available online at https://www.nps.gov/yell/learn/nature/upload/2008_IBMP_AMP.pdf (accessed January 4, 2017).
- IBMP. 2012. 2012 Annual Report of the Interagency Bison Management Plan. Available online at <http://ibmp.info> (accessed May 25, 2017).
- IBMP. 2014. IBMP Adaptive Management Plan. Available online at <http://www.ibmp.info/adaptivemgmt.php> (accessed January 4, 2017).
- Kauffman, M., K. Boroff, D. Peck, B. Scurlock, W. Cook, J. Logan, T. Robinson, and B. Schumaker. 2013. Cost-benefit Analysis of a Reduction in Elk Brucellosis Seroprevalence in the Southern Greater Yellowstone Area. University of Wyoming.
- Lubow, B., and B. Smith. 2004. Population dynamics of the Jackson elk herd. *Journal of Wildlife Management* 68:810-829.
- Maichak, E.J., B.M. Scurlock, P.C. Cross, J.D. Rogerson, W.H. Edwards, B. Wise, S.G. Smith, and T.J. Kreeger. 2017. Assessment of a strain 19 brucellosis vaccination program in elk. *Wildlife Society Bulletin* 41:70-79.

Revisiting Brucellosis in the Greater Yellowstone Area

- Mao, J.S., M.S. Boyce, D.W. Smith, F.J. Singer, D.J. Vales, J.M. Vore, and E.H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. *Journal of Wildlife Management* 69:1691-1707.
- Martin, J., M.C. Runge, J.D. Nichols, B.C. Lubow, and W.L. Kendall. 2009. Structured decision making as a conceptual framework to identify thresholds for conservation and management. *Ecological Applications* 19:1079-1090.
- McCarthy, M.A., and J.P. Possingham. 2007. Active adaptive management for conservation. *Conservation Biology* 21:956-963.
- Millsbaugh, J.J., R.A. Gitzen, D.R. Larsen, M.A. Larsen, and F.R. Thompson, III. 2008. General principles for developing landscape models for wildlife conservation. Pp. 1-32 in *Models for Planning Wildlife Conservation in Large Landscapes*. J.J. Millsbaugh, and F.R. Thompson, III, eds. Amsterdam, The Netherlands: Elsevier.
- NRC (National Research Council). 1998. *Brucellosis in the Greater Yellowstone Area*. Washington DC: National Academy Press.
- NRC. 2004. *Adaptive Management for Water Resources Project Planning*. Washington, DC: The National Academies Press.
- Olsen, S.C., S.J. Fach, M.V. Palmer, R.E. Sacco, W.C. Stoffregen, and W.R. Waters. 2006. Immune responses of elk to initial and booster vaccinations with *Brucella abortus* strain RB51 or 19. *Clinical and Vaccine Immunology* 13(10):1098-1103.
- Reever Morghan, K.J., R.L. Sheley, and T.J. Svejcar. 2006. Successful adaptive management—the integration of research and management. *Rangeland Ecology and Management* 59(2):216-219.
- Roffe, T.J., L.C. Jones, K. Coffin, M.L. Drew, S.J. Sweeny, S.D. Hagius, P. Elzer, and D. Davis. 2004. Efficacy of single calfhoo vaccination of elk with *Brucella abortus* strain 19. *Journal of Wildlife Management* 68(4):830-836.
- Sandifer, P.A., A.E. Sutton-Grier, and B.P. Ward. 2015. Exploring connections among nature, biodiversity, ecosystem services, and human health and well-being: Opportunities to enhance health and biodiversity conservation. *Ecosystem Services* 12:1-15.
- Schumaker, B. 2015. *Brucellosis Diagnostics and Risk. Assessment for Wildlife & Livestock Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area*, September 16, 2015, Jackson Lake Lodge, WY.
- Scurlock, B. 2015. *Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area*, September 16, 2015, Jackson Lake Lodge, WY.
- Taper, M.L., and P.J.P. Gogan. 2002. The northern Yellowstone elk: Density dependence and climatic conditions. *Journal of Wildlife Management* 66:106-122.
- Thorne, E.T., T.J. Walthall, and H.A. Dawson. 1981. Vaccination of elk with strain 19 *Brucella abortus*. *Proceedings of U.S. Animal Health Association* 85:359-374.
- USDOI/USDA (U.S. Department of the Interior and U.S. Department of Agriculture). 2000a. Final environmental impact statement for the Interagency Bison Management Plan for the state of Montana and Yellowstone National Park.
- USDOI/USDA. 2000b. Record of Decision for Final Environmental Impact Statement and Bison Management Plan for the State of Montana and Yellowstone National Park, December 20, 2000. U.S. Department of the Interior, National Park Service, and U.S. Department of Agriculture, U.S. Forest Service, Animal and Plant Health Inspection Service. Available online at <https://www.nps.gov/yell/learn/management/upload/yellbisonrod.pdf> (accessed January 4, 2017).
- USFWS/NPS (U.S. Fish & Wildlife Service and National Park Service). 2007. *Bison and Elk Management Plan for the National Elk Refuge and Grand Teton National Park*. Available online at <http://www.fws.gov/bisonandelkplan> (accessed January 4, 2017).
- Varley, N., and M.S. Boyce. 2006. Adaptive management for reintroductions: updating a wolf recover model for Yellowstone National Park. *Ecological Modelling* 193:315-339.
- Walters, C.J. 1986. *Adaptive Management of Renewable Resources*. New York: Macmillan. 374 pp.
- Walters, C.J., and C.S. Holling. 1990. Large-scale management experiments and learning by doing. *Ecology* 71:2060-2068.
- Westgate, M.J., G.E. Likens, and D.B. Lindenmayer. 2013. Adaptive management of biological systems: A review. *Biological Conservation* 158:128-139.
- Williams, B.K. 2011. Passive and active adaptive management: Approaches and an example. *Journal of Environmental Management* 92:1371-1378.

Adaptive Management

Williams, B.K., R.C. Szaro, and C.D. Shapiro. 2009. Adaptive Management: The U.S. Department of the Interior Technical Guide. Available online at <https://www2.usgs.gov/sdc/doc/DOI-%20Adaptive%20ManagementTechGuide.pdf> (accessed May 25, 2017).

7

Management Options

1. INTRODUCTION

Management actions are “tools” that can be used to reduce the risk of brucellosis transmission and to mitigate the effects of infection in the Greater Yellowstone Area (GYA). This chapter provides a brief overview of various approaches that have been used and are available for stakeholders in managing the risk of *Brucella abortus* transmission. These management tools can and will need to be used in combination as part of an active adaptive management approach.

2. INCENTIVIZING RISK MITIGATION EFFORTS

One way to affect change would be to provide incentives for action. In the context of managing brucellosis, it could take the form of incentivizing cattle producers either to undertake risk mitigating efforts and decisions or to adjust the time or location for allowing cattle to graze on public or private lands. These two options are discussed in more detail in Chapter 8. Two other tools include (1) adjusting governmental fixed rate and placement date approaches to public grazing and (2) an insurance approach to help protect producers against damages. These are also discussed briefly in Chapter 8 and are expanded on below.

2.1 Adjusting Governmental Fixed Rate and Placement Date Approaches

Public efforts could be better aligned to encourage certain outcomes. One option would be to compensate cattle producers whose herds become infected in direct proportion to their risk mitigation efforts. A producer could be compensated by the government in “full” if they provide evidence that they have implemented a set of “best management practices” for reducing brucellosis risk. Conversely, if a producer is able to provide only partial evidence of “good faith behavior,” then only some proportion of compensation would be available (e.g., if a producer in the GYA elected to not fence off their haystacks, they may then be eligible for only a proportion of the compensation level deemed available for brucellosis based testing and damages). Indemnity claims have been used for other diseases—the U.S. Department of Agriculture’s Animal and Plant Health Inspection Service (USDA-APHIS) has regulations to specify conditions for payment of indemnity claims for low pathogenic avian influenza (LPAI)—and a similar approach could also be considered as a possible tool for brucellosis. However, care will need to be taken as the core role of indemnity compensation is to encourage timely and complete reporting by reducing the economic incentive to censor information on disease events.

The establishment of public grazing fees and cattle placement dates also warrants further consideration. Parcels vary in risk depending on their location, the presence or absence of elk, and the time of year. Currently, the fixed rate (updated annually) and entry date for federal grazing makes no consideration of brucellosis risks (Rimbey and Toreel, 2011). For example, one parcel next to an elk feedground with no fences will be riskier than another that is further away with fences; however, the federal grazing rate for both parcels is the same even though the brucellosis exposure risk is different across the two parcels. This is a classic example of an economically inefficient, fixed rate pricing program that fails to reflect the different impacts public grazing has on broader brucellosis risks in the area. The committee acknowledges the political challenges that may arise with a differential grazing rate system, yet the fixed rate approach fails

Management Options

to account for risks and external costs. Even if a differential pricing system is infeasible upon further assessment, it will be essential to restrict or adjust the placement and removal dates to reflect parcel-specific brucellosis risk. If cattle were allowed to graze on “high risk” public lands with earlier placement remaining available on “lower risk” parcels, producer actions would more directly internalize brucellosis risks currently not captured by the fixed pricing and entry date system. To date, risk categorization of public lands has yet to be clearly defined and a risk assessment is clearly needed. (See Box 7-1 for an example of land managers using a risk assessment to reduce contact between Sierra Nevada bighorn sheep and domestic sheep.)

Federal land management agencies could stipulate risk reduction “best management practices” in exchange for the privilege of using public land grazing allotments. Although an individual producer may not view these practices as necessary or cost-effective, reducing risk of transmission between elk and cattle in the GYA is in the public interest. Therefore, this would be another area where policies could be used to incentivize best practices. By considering additional private incentives, it may be possible to encourage private action to better align with the broader public interest.

2.2 Insurance

Insurance for livestock diseases provides monetary relief to producers, as some losses—business interruption, welfare (feeding and care) costs for animals, and loss of markets—are not currently eligible for U.S. government indemnification (Grannis et al., 2004). Insurance premiums subsidies could be tied to evidence of implementing best management practices, a concept reflected in USDA’s recent adjustments to highly pathogenic avian influenza indemnity payments to poultry producers (USDA-APHIS, 2016). For example, producers in the GYA could be eligible for an insurance premium discount if they wait until late June to place cattle on public lands when the risk from elk is lower. Although the concept of an insurance program is sound, there are a host of challenges to making it viable, including knowledge gaps in accurately assessing risk, whether there is sufficient interest by producers, and the government’s capacity to administer and subsidize premiums (Goodwin and Smith, 2013; Reeling and Horan, 2014). Also, livestock producers tend to implement even less costly risk management strategies than expected (Goodwin and Schroeder, 1994; Pennings and Garcia, 2001; Wolf and Widmar, 2014). Information is currently lacking to assess the viability of either a new insurance program or an alternative compensation program. Insurance programs are not prevalent in livestock disease prevention programs, but indemnity programs are (Hoag et al., 2006; USDA-APHIS, 2016).

3. USE OF FEEDGROUNDS

Efforts to feed wildlife can range from individual efforts (such as backyard birdfeeders and baiting on private property to aid in hunting) to state-sponsored programs that feed large ungulates across the western United States (Smith, 2001; Sorensen et al., 2014). Supplemental feedgrounds for elk and bison in Wyoming are some of the largest-and-longest operating efforts. The original intent of feedgrounds was both to buffer against starvation in severe winters (as traditional winter feed areas had been developed into cattle ranches) as well as to limit the losses of hay on private properties due to elk (Smith, 2001). A third reason for the feedgrounds is to reduce the likelihood of disease transmission by maintaining a separation between elk and cattle. However, counter to that purpose, supplemental feeding increases elk and bison aggregations and facilitates brucellosis transmission within these populations (NRC, 1998; Cross et al., 2007). Although the intent is to minimize the chance of spillover to cattle, feedgrounds may exacerbate the problem by increasing seroprevalence in elk, not only in the southern GYA but also in other portions of the GYA. While there are aesthetic or philosophical arguments for or against the feedgrounds, this report confines the examination of feedgrounds to their role in either facilitating or limiting the spread of brucellosis both within and between host species as well as their potential role in the future management of brucellosis.

*Revisiting Brucellosis in the Greater Yellowstone Area***BOX 7-1** Land Management Risk Assessment to Reduce Disease Risks

Risk assessments can be useful by allowing land managers to identify and assess risk and to evaluate management options for mitigating that risk. In the case of Sierra Nevada bighorn sheep, risk modeling was conducted to predict the effectiveness of various efforts to reduce contact between bighorn sheep and domestic sheep, which can lead to outbreaks of fatal pneumonia in bighorns (Clifford et al., 2009). Several management options were compared including trucking versus trailing, use of guard dogs, and modified grazing times and locations. The model predicted that restricting grazing time on allotments perceived as high risk would result in a 76%-82% reduction in the annual probability of a pneumonia case for the Northern area and would have the most impact on reducing risk of disease transmission (Clifford et al., 2009).

In the case of brucellosis, risk modeling could also be useful for identifying the areas of highest risk for brucellosis transmission and for determining the effectiveness of modifications in grazing allotments to reduce contact between cattle and elk. As part of such a risk assessment, the costs associated with various actions can also be compared to the level of risk reduction. The U.S. Forest Service and the Bureau of Land Management could similarly undertake risk assessments to help land managers determine where and when to restrict grazing that will optimize risk reduction of brucellosis transmission from elk to bison.

SOURCE: Clifford et al., 2009.

Supplemental feedgrounds have exacerbated brucellosis in elk and bison, facilitated the spread of brucellosis across the GYA, and increased the risk for the introduction of other diseases (such as chronic wasting disease [CWD] or bovine tuberculosis). Brucellosis isolates taken from elk and livestock outside of Yellowstone National Park (YNP) had genetic ancestors from the feedgrounds rather than bison from Yellowstone (Kamath et al., 2016). Although the current genetic data suggest that the supplemental feedgrounds likely sparked several outbreaks in distant elk populations, the rare dispersal events between populations are unlikely to maintain the high seroprevalence of the disease currently observed in many free-ranging elk populations (Cross et al., 2010a). Despite the potential drawbacks of feedgrounds, they do provide some management opportunities. First, the number of cattle outbreaks in counties with supplemental feedgrounds appears to be no higher than in areas without supplemental feedgrounds (Brennan, 2015). This suggests that feedgrounds may contribute to maintaining spatial separation between cattle and elk even though they exacerbate disease in the elk population. Second, feedgrounds make elk more accessible either for vaccination or for capture in corral traps or darting from the ground. Feedgrounds could thus be used as a test case for management action. One example is for sterilizing elk that are likely to abort (presumably young age seropositive females that may be in their first or second pregnancy), which would slow the transmission of brucellosis and subsequently reduce elk seroprevalence over time.

Ecologically oriented management actions may also help mitigate feedground associated problems. Feeding elk later in the spring tends to be associated with higher seroprevalence: an additional 30 days of feeding was associated with a two- to three-fold increase in seroprevalence, as abortions and calving are more likely to occur in the spring (Cross et al., 2007). However, the winter population size at the feedgrounds was not a significant predictor of seroprevalence, which may be due to an interaction between density and timing of transmission; if so, transmission occurring later in the spring would be less dependent on feedground elk density in the winter (Maichak et al., 2009). These results have prompted the Brucellosis-Habitat-Feedground Program at the Wyoming Game & Fish Department (WGFD) to attempt to implement a test program of ending the feeding season earlier on some feedgrounds to test the causal link between the length of the feeding season and the resulting elk seroprevalence. Even if this management action is successful, it is potentially not without trade-offs. Even if elk seroprevalence declines, it is unclear whether cattle risk may be reduced because additional elk-cattle contact outside of the feeding season may occur. Thus, there may be short-term risks of local elk-cattle spillover around the feedgrounds prior to realizing the potential long-term benefits of reduced elk seroprevalence. Feeding hay in a more widely distributed

Management Options

style is another approach that has been shown to markedly reduce elk-fetus contacts (Creech et al., 2012). This treatment is being implemented on several feedgrounds, but it remains to be seen whether it results in reduced elk seroprevalence.

At the time of the 1998 NRC report, brucellosis was limited to bison and the Wyoming supplemental feedgrounds, and therefore a recommended phase-out of the feedgrounds appeared to be a means toward wide-scale disease reduction in elk. This is no longer the case as elk populations distant from both bison and elk appear to maintain the infection, and management actions on feedgrounds are unlikely to have ramifications for distant elk populations (e.g., Montana elk, as well as the Cody and Clarks Fork regions of Wyoming) given that the disease is already present in those populations. However, reductions on the feedgrounds may be beneficial for reducing potential spread to other regions, such as northeastern Utah where another supplemental feedground operates. Several nongovernmental organizations have argued for the complete phasing out of supplemental feedgrounds for a number of reasons, including CWD. If this were to be considered, feeding could first be curtailed at the most cattle-sensitive feedgrounds with the expectation that elk would move to less sensitive feedgrounds prior to a complete phaseout. As noted above, feedground closures are likely to have short-term costs due to the potential for increased elk-cattle contact while the seroprevalence in elk remains high, yet the long-term benefits could include reduced elk seroprevalence. Feedgrounds appear to mitigate some of the cattle risk locally while enhancing disease risks across the ecosystem (for *B. abortus*, CWD, and other diseases).

The concentration of elk and bison on supplemental feedgrounds has been associated with a number of diseases in addition to brucellosis, which led to a recent court case against the U.S. Fish & Wildlife Service (USFWS) for allegedly failing in its mandate to promote “healthy” wildlife (*Defenders of Wildlife et al. v. Salazar*, U.S. App. D.C., No.10-1544[2011]). More than half of the adult male elk that die on the National Elk Refuge (NER) annually were infected with scabies, while only 5% of surviving adult males showed clinical signs (Smith and Anderson, 1998). In addition, the management units with feedgrounds had variable calf ratios, indicating no clear support for generally higher ratios in areas with supplemental feedgrounds (Foley et al., 2015). Elk attending the feedgrounds had higher fecal glucocorticoids (FGCs)—hormones associated with stress—than elk that were on native winter ranges (Forristal et al., 2012). These FGCs also appeared to be correlated with the local density of elk at each site. Although glucocorticoids are known to be immunosuppressive, it remains undetermined how these levels of FGCs relate to other factors such as disease susceptibility, survival, or recruitment. Meanwhile, results from the analysis of *Brucella* isolates suggest that the feedgrounds are the likely source for elk infections in other areas of the GYA, with the exception of the Paradise Valley in Montana (Kamath et al., 2016).

Finally, CWD is often a major point of discussion with supplemental feeding programs (Smith, 2013). CWD is a transmissible spongiform encephalopathy that infects elk, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), and moose (*Alces alces*) (Williams and Young, 1980; Williams, 2005). It can be transmitted by direct contact or indirectly via the deposition of prions in feces, saliva, and urine in the environment. Several studies suggest that these prions persist in the environment for years (Miller et al., 2004; Mathiason et al., 2006). While the prevalence of CWD in free-ranging elk tends to be much lower than in either white-tailed or mule deer, the supplemental feedgrounds may represent a worst-case scenario that is more similar to the high potential for rapid spread in captive elk herds where prevalence can be quite high. CWD may have dramatic effects on the elk populations visiting the supplemental feedgrounds, but those effects are likely to occur over long timescales (e.g., 20-40 years) (Wasserberg et al., 2009; Almberg et al., 2011).

4. HUNTING OF WILDLIFE

Hunting is often cited as the foundation for the system of wildlife management in North America (Heffelfinger, 2013). Unhunted wild ungulate populations—particularly in the absence of predators or other natural mortality factors—often overpopulate their habitat to a point that negatively impacts forage production, causes detrimental changes in the ecosystem, reduces ungulate carrying capacity, and causes conflicts with humans (e.g., agricultural losses and vehicular accidents) (Conover, 2001). When ecosystem-

Revisiting Brucellosis in the Greater Yellowstone Area

level effects are seen, reproduction may decrease and mortality increase due to competition for remaining resources (McCullough, 1979). Hunting is sustainable as long as off-take does not exceed reproductive and survival capacity of the next generations. Overhunting was the cause of severe depletion (elk deer, antelope, bighorn sheep) and near extinction (bison) of many game species in North America in the late 19th century (Heffelfinger, 2013).

The distribution and abundance of wildlife can be changed by manipulating hunting pressure and its spatial distribution (Conner et al., 2007). Public hunting can be used to alter numbers of free-ranging wild ungulates (deer, elk, antelope, and bison), population densities, and sex ratios (Heffelfinger, 2013). However, public hunting is not a precise tool and has significant limitations when targeting specific populations, particularly if target animals are not easily identifiable in the field or are not on accessible lands. Despite initial enthusiastic cooperation by hunters, efforts to use hunting to reduce or eliminate chronic wasting disease in white-tailed deer in Wisconsin failed due to several factors, including waning enthusiasm for the program and too little progress in reducing infection rates (Jennelle et al., 2014). This demonstrates how hunting can be a limited tool for disease reduction purposes.

4.1 Hunting and Disease Control in the GYA

The management of wildlife is primarily the legal responsibility of state and federal governments, and hunting of wildlife generally falls under the jurisdiction of state wildlife management agencies (Krausman, 2013). Each state sets seasons and bag limits on a herd-by-herd basis through Herd Management Plans (HMPs) (MDFWP, 2015; WGFD, 2015). The results of the previous year's harvest, field observations, and marking studies (otherwise known as the marked capture/recapture index) of selected herds are used to set HMP goals (MDFWP, 2015). There are instances in which hunting is allowed on federal parks and refuges. A limited elk hunt is allowed at the eastern edge of Grand Teton National Park (Consolo-Murphy, 2015). Elk and bison are taken by hunters on the NER, which is managed by the USFWS. YNP does not allow hunting. Hunting access is allowed on most Bureau of Land Management (BLM) and U.S. Forest Service (USFS) lands and a large portion of the GYA, while hunting on private lands is managed by their owners.

Hunting could be used to reduce disease transmission risk by reducing elk populations in areas where prevalence of brucellosis is relatively high, where incidence of infection appears to be increasing, and where there is greater risk of contact with cattle. Increasing the proportion of female elk harvested yearly can help reduce elk herd numbers and the number of potentially infectious females. Late-season antlerless hunts could also reduce the number of female elk numbers and proportion of infected females, decrease the herd growth rate, and possibly break up dense aggregations of elk. This has been done to some extent in Wyoming. However, it is difficult for hunters to identify and specifically target brucellosis-infected elk or bison. There are also temporal (e.g., seasons), physical (e.g., weather, terrain), and legal (e.g., private lands) barriers that may limit the effectiveness of hunting as a disease-control tool. A significant barrier to wider applications of hunting for brucellosis management is the complex land ownership pattern that results in elk refugia forming on un hunted private lands during hunting seasons. Informational outreach, incentives, and a case for hunting as a disease-control tool may need to be made.

When disease transmission is correlated with host density as it is with brucellosis, disease agents may be unable to persist if densities are lowered beyond a critical threshold. In wildlife systems, however, those thresholds are difficult to define and there is countervailing evidence that merely decreasing elk population size alone may not decrease seroprevalence enough to warrant management changes (Lloyd-Smith et al., 2005; Cross et al., 2010b; Proffitt et al., 2015).

A secondary benefit of hunting in areas where elk populations exceed herd management goals could be to ensure against catastrophic winter kill in years of extreme weather. Hunting is a management tool to be used with caution because increasing hunter tags at a broad regional scale may shift elk distributions to areas of limited hunter access and thus intensify conflict on private lands or drive elk to un hunted (refuge) private lands.

Blood samples can help track brucellosis exposure, and hunters are often willing to collect blood samples from harvested animals to assist wildlife management agencies. The quality of samples and the

Management Options

accuracy of location information have unfortunately been less than optimal for hunter-collected blood samples provided to WGFD. The Montana Department of Fish, Wildlife & Parks has ceased using hunter-collected blood samples in favor of samples collected from elk captured for marking and herd studies. But, as seen with recent cases of brucellosis on the Montana-Wyoming border near the Bighorn Mountains, targeted hunter sampling (as opposed to general sampling) could help in monitoring brucellosis at the DSA border and just beyond.

4.2 Economic Considerations

Hunting and harvesting elk and bison (and other wildlife) in the Greater Yellowstone Ecosystem is a source of income for individuals and small businesses (USFWS, 2012). Many in Idaho, Montana, and Wyoming would even consider access to public lands for hunting a right, and the view the harvesting of an elk (or a deer, an antelope, and, to a lesser extent, bison) as a yearly necessity for food security. Native Americans have the legal right to harvest wildlife under various treaties (Organ, 2013). Although no hunting occurs within the boundaries of YNP, bison culls and hunts do occur when bison move out of YNP and into the Gardiner Valley and along the western YNP boundary. Bison that are not part of YNP herds are hunted on public and private lands in Montana and Wyoming.

State game and fish departments derive a significant portion of income from hunting, with elk hunting revenue being one of the largest single sources of revenue for the game and fish departments in Idaho, Montana, and Wyoming (Heffelfinger, 2013). In 2009, there were 62,620 elk-hunting licenses sold in Wyoming, which resulted in \$8,649,005 in license sales alone, approximately 50% of revenue for WGFD. The cost to WGFD was \$638 per animal, with net income to WGFD of \$1,765 per animal. During the hunting season, hunters use the full array of local business services and amenities (such as gas, food, lodging, sporting goods and equipment). In 2006, 762,000 people spent a total of \$1.1 billion to take part in wildlife associated recreation in Wyoming (USFWS, 2012). Of these, 84% reported participating in wildlife watching, 13% participated in hunting, and 3% indicated other (undisclosed). Of the money spent, 44% were trip-related expenses (e.g., fuel, hotels). The committee received public comments from ranchers in the GYA who are part-time hunting guides and derive significant income from these activities, and ranchers also noted that they charge access fees to allow hunters on their property. It is interesting to note that for Wyoming in 2010, the aggregate gross value of cattle ranching for the entire state (\$1.24 billion) is only slightly higher than the amount spent on wildlife-related recreation (\$1.1 billion) (USDA-NASS, 2010). Nationwide, the money generated by regulated sport hunting and the incentives it provides for wildland conservation is generally credited with being the primary reason for the recovery of elk, antelope, and deer populations and—to a lesser degree—bison in the last century (Heffelfinger, 2013). Therefore, a major reduction in elk numbers for brucellosis control could potentially be in direct conflict with the interests of state game and fish departments.

Intense hunting activities involving brucellosis-infected bison or elk could elevate the public health risk if carcasses and offal are not removed. Approximately 50% of the bison that leave YNP enter the Gardiner, Montana, area in late winter and are subject to intensive hunting pressure in a relatively small geographic area. Testimony and photos were provided to the committee during a public comment session noting instances in which bison carcasses were left in close proximity to populated and public areas. The failure to remove carcasses and “gut piles”—including the lymphoid organs and reproductive tracts of animals—constitutes a potential health risk to the public, domestic livestock, and companion animals. Timely removal and proper disposal of post-harvest animal remains could also help build public support for the Interagency Bison Management Plan (IBMP) hunts.

In the past few decades, some prime hunting and ranching lands (particularly in Montana, north and northwest of YNP) have been purchased by individuals who do not support hunting (Haggerty and Travis, 2006). These are often large tracts of land that serve as refuges for elk and complicate efforts to regulate elk numbers by hunter harvest (Haggerty and Travis, 2006; MDFWP, 2015). Elk habituating to use of private protected lands significantly compromises the ability of state wildlife agencies to use hunting as a tool to manage elk numbers.

*Revisiting Brucellosis in the Greater Yellowstone Area***5. LAND USE****5.1 Brucellosis Management Action Plans**

Brucellosis Management Action Plans (BMAPs) have been developed to consider a wide range of efforts aimed at addressing brucellosis in a more holistic fashion. Many of these BMAPs have been developed to address brucellosis by species (either elk or bison). For example, the Jackson elk herd BMAP states its objectives are to “maintain livestock producer viability, reduce/eliminate dependence of elk on supplemental feed, maintain established elk herd unit objectives, improve range health, and maximize benefits to all wildlife” (WGFD, 2011). A BMAP identifies the pros and cons for various options, including fencing, habitat improvement, conservation easements, and switching from cow-calf operations to stocker operations. The BMAP also acknowledges that for any action, such decisions would be under the purview of various stakeholders, including state agencies and individual producers. Land acquisition and conservation easements would involve buying or long-term leasing of land, with decision authority resting with private landowners; transactions involving WGFD (e.g., conservation easements) would have to proceed ultimately through that state agency (WGFD, 2011).

Land acquisition for winter range outside YNP remains a goal for many stakeholders interested in bison welfare, habitat to support the free-roaming nature of bison, and less invasive management actions. Land acquisition and deactivation of livestock grazing allotments have proven to be successful not only at providing bison with more habitat but also in reducing risks associated with bison-livestock interactions. As has occurred under the IBMP, acquisition of bison winter range is achieved through purchase of grazing rights, easements, or property from landowners and livestock producers, thus providing them with economic compensation.

A BMAP for the Jackson bison herd was developed by WGFD in cooperation with the National Park Service (NPS) and USFWS (WGFD, 2008a). The BMAP outlines efforts to conserve and improve habitats, minimize bison/elk conflicts with adjacent landowners, provide for a feeding program co-managed with WGFD, and a structured framework of adaptive management in collaboration with the WGFD to transition from intensive supplemental winter feeding to greater reliance on natural forage. The BMAP calls for WGFD to work with the Wyoming Livestock Board to keep bison and cattle separated through several actions, such as hazing as appropriate and fencing. It also calls for WGFD to work with managers on the NER and USFS lands to use hunting to maintain a population objective. The BMAP also calls for habitat enhancement, shorter feeding durations, and feeding in fewer years to reduce risk of intraspecies transmission. A bison BMAP has also been developed for the Absaroka Bison Management Area to address the few bison that wander from the YNP herd and exit the eastern boundary of YNP (WGFD, 2008b). This BMAP calls for many of the same management options as in the Jackson BMAP, particularly efforts to maintain separation of bison from livestock. The IBMP has been successful in managing bison, but it is not considered a BMAP as it does not directly address brucellosis.

Livestock producers in the GYA have been working with federal and state management agencies to reduce risks of transmission to their herds. Management efforts are developed as part of herd management plans for the designated surveillance areas (DSAs). For its BMAP, WGFD has suggested management options for fencing the elk and bison herds away from cattle in Wyoming. WGFD has also suggested that the timing of cattle grazing on Bridger-Teton National Forest and Grand Teton National Park grazing allotments be manipulated to achieve temporal and spatial separation of bison and cattle. The same principle would also apply to managing the timing of cattle grazing on allotments throughout the GYA and within DSAs that are permitted by USFS and BLM. The Cody herd BMAP provides management actions to redistribute elk and reduce negative impacts of land ownership on elk distributions and hunter access (WGFD, 2012). These proposed actions include working with landowners to maintain access for hunters to meet harvest objectives (possibly through an incentive program); reducing or dispersing large groups of elk adjacent to and on private lands; and preventing the comingling of elk and cattle during high-risk periods, which requires WGFD to cooperate with landowners to move elk away from cattle. Similar management actions would be useful throughout the broader GYA.

*Management Options***5.2 Biosecurity (Spatial-Temporal Separation)**

Biosecurity is defined as “the implementation of measures that reduce the risk of disease agents being introduced and spread” (FAO, 2010). Biosecurity measures are used to prevent the entry of pathogens into a herd or farm (external biosecurity); if a pathogen is already present, biosecurity measures are used to prevent the spread of disease to uninfected animals within a herd (internal biosecurity).¹ Biosecurity is one of the most important considerations in preventing brucellosis from getting into a cattle herd, especially given the presence of free-ranging wildlife. Biosecurity measures within the GYA are focused on external biosecurity, specifically the separation of cattle from elk and bison. Examples of practices recommended by state and local agencies include fencing of haystacks, testing cattle prior to adding them to the herd, and not moving breeding stock to risky summer range until after mid-June.

USDA-APHIS conducts National Animal Health Monitoring System (NAHMS) surveys that document the national adoption rates of biosecurity-related practices. The NAHMS surveys consistently find that many biosecurity measures are only partially implemented by producers despite strong, long-standing recommendations from experts. Although there is some available research that investigates necessary biosecurity and security practices for operations outside the GYA (Brandt et al., 2008), little is known about the factors affecting producers’ willingness to implement protective practices because literature related to brucellosis for the GYA is limited. There are estimates on the costs of implementing brucellosis prevention activities on a representative cow/calf-long yearling operation, which provides a break-even analysis from the producer’s perspective (Roberts et al., 2012). However, analysis is lacking that captures a germane discussion of public goods and externalities for the GYA. Furthermore, the actual implementation rate of brucellosis-focused biosecurity practices in the GYA remains unknown.

Cattle producers in the GYA incur additional expenses when implementing biosecurity measures, which they consider costly as “it just makes doing business in this part of the world much harder” (Lundquist, 2014; Rice, 2015). The costs and benefits of implementing a specific biosecurity measure may vary across producers, yet this has not been fully documented. For instance, a producer bordering an elk feedground faces different private benefits while a producer with more “home ranch” summer range options faces lower costs of delaying movement of cattle onto higher-risk, external summer range. Moreover, the impact of a given producer’s actions on other producers is not well documented yet is critical to understand (Peck, 2010). This ties directly to externalities and the need for a broader bioeconomic modeling that considers more than just private aspects of these decisions (see Chapter 8 on bioeconomics).

7. ZONING USING DESIGNATED SURVEILLANCE AREAS

The Brucellosis Eradication Program formerly relied on a state-by-state approach (defined by geopolitical areas and boundaries) for classifying brucellosis status in the United States. States with no cases of brucellosis in livestock (zero prevalence) for at least a year with documented surveillance were classified as Class Free states. Interstate movement requirements and associated testing costs to producers became less burdensome as a state’s status was upgraded (9 CFR Part 78, 2006). This approach worked well because there was an incentive for livestock producers to work with states to eliminate brucellosis and thus reduce or eliminate costs associated with testing. All 50 states were briefly recognized as free of brucellosis in 2008. It was then recognized that the identification of only a few cases of brucellosis in livestock in a small geographic area, such as the GYA, could result in loss of Class Free status for the entire state. Increased testing costs associated with loss of status would then be unnecessarily and inefficiently borne by all producers, even though the majority of the cattle herds resided in low-risk areas of the state far from the risk of infection. Politically challenging surveillance and disease-control approaches were often quickly implemented in an effort to regain statewide Class Free status.

¹When applied to biosecurity, the modifiers “internal” and “external” differ from the modifiers “internal” and “external” when applied to economic impacts, as further described in Chapter 8.

Revisiting Brucellosis in the Greater Yellowstone Area

DSAs were introduced by USDA-APHIS in a 2009 concept paper as a zoning approach for addressing brucellosis and were implemented in a 2010 interim rule (USDA-APHIS, 2009; 75 Federal Register 81090 [2010]). A regionalization approach that defines brucellosis risk areas and is consistent with World Organisation for Animal Health standards creates several advantages, including the ability to focus resources specifically in high-risk areas and increased flexibility in modifying the boundaries of the disease management area to reflect changes in risk while still assuring trading partners of the brucellosis-free status for the remainder of the country.

The success of the DSA concept relies on at least two important surveillance streams. First, it is dependent on adequate surveillance in wildlife. The DSA encompasses areas with endemic brucellosis in wildlife populations; thus, surveillance on the DSA perimeter will need to be adequate to delineate the area of risk to livestock species and determine the appropriate boundaries for the DSA. With financial support from USDA, state wildlife and animal health agencies cooperate to conduct surveillance in wildlife. Second, the concept of zoning relies on sufficient surveillance to detect brucellosis in livestock within and leaving the DSA. Adult breeding cattle are tested as they leave the DSA or as they change ownership within the DSA, but there are exceptions in some states for livestock consigned to slaughter.

State animal health agencies are responsible for designating the boundaries of their DSA and describing their rationale via a Brucellosis Management Plan (BMP) that is subsequently approved by USDA. Idaho, Montana, and Wyoming have BMPs, yet they have varied approaches in meeting these two critical surveillance needs. DSA testing requirements have led to the disclosure of 16 herds with brucellosis in the GYA since the DSAs were implemented. Each of the GYA states has consequently adjusted its DSA boundaries at least once since initial designation because of seropositive elk. The lack of uniformity in how states conduct surveillance, determine appropriate expansion of DSAs, and enforce DSA boundaries may be a hindrance to rapid identification and adequate mitigation of infection. As previously mentioned in Chapter 5, these and other gaps in the management of animals leaving the DSA will need to be addressed for the regionalization approach to be effective in addressing brucellosis (USAHA, 2012).

8. TEST AND REMOVE

Testing and removal of brucellosis seropositive animals is a critical component of a strategy for eliminating brucellosis from an affected population. Test and remove is one of many tools that has been used in a variety of ways and to various degrees of success; however, it is rarely effective if used alone. To reduce the possibility of transmission, seropositive animals in an affected population would need to be removed from the herd and maintained separately from negative animals, or removed to either slaughter, research, or to a properly monitored quarantined feedlot, if available. The failure to remove seropositive animals likely results in continued transmission and an inability to control the disease. A major factor to reduce exposure and transmission of brucellosis is detecting and removing infected cows prior to parturition (Nielsen and Duncan, 1990). High-risk animals, such as exposed bred heifers, are sometimes removed as part of a brucellosis elimination strategy to ensure that they do not seroconvert and continue to spread the disease. In addition, highly susceptible seronegative animals are sometimes maintained separately to prevent exposure and subsequent infection.

In livestock populations, testing and removal alone without any other disease mitigation efforts—and especially testing and removal without consideration of the time of calving and abortion—has not proven to be an effective strategy (Caetano et al., 2016). However, testing and removing seropositive animals is an effective tool when properly utilized as part of a disease-control or elimination strategy. Three major strategies have been demonstrated to be effective tools to control brucellosis in livestock when used in combination with other tools: (1) strict biosecurity at the farm level, including herd management to minimize the risk of contact with viable *Brucella* (such as calving management, separating replacement heifers and managing them as a separate unit, increasing biosecurity so as to protect herds from purchasing infected animals or becoming infected from community herds, and utilizing cleaning and disinfecting when appropriate to minimize environmental contamination); (2) vaccination; and (3) testing and removal programs (Pérez-Sancho et al., 2015).

Management Options

In the United States, considerable progress was made toward eliminating brucellosis from cattle by replacing blind test and slaughter methods of the 1970s with the development of individual herd plans (Adams, 1990). These herd plans included the use of additional disease mitigation actions such as vaccination and separation of high-risk animals to reduce transmission and limit exposure of naïve animals. Vaccination alone is insufficient to eradicate brucellosis, but it increases resistance to infection and it reduces both the risk of abortions and the excretion of *Brucella* (European Commission, 2009). The key to success, however, is to test and rapidly remove infected animals before they have the opportunity to continue to transmit the disease (PAHO, 2001).

In some countries, when the prevalence of brucellosis is high or socioeconomic resources are limited, mass vaccination is the most suitable tool for the initial control of the disease (Pérez-Sancho et al., 2015). In those cases, systemic and mandatory vaccination is used to reduce infection rate to a level where testing and removal can then be used to eradicate the disease. For brucellosis, it is estimated that 7-10 years of systemic vaccination are necessary to achieve this objective (PAHO, 2001).

In several cases with both privately and publicly owned bison herds, a testing and removal strategy has been used in combination with other management actions to eliminate brucellosis. In combination with vaccination, the test and remove strategy has been effectively used for brucellosis in bison in the following six cases:

1. Test and removal, combined with vaccination, was previously used in YNP in the early 1900s and reduced the seroprevalence of bison from 62% to 15% in 2 years (Coburn, 1948).
2. In 1961, the Henry Mountain bison herd in Utah was declared free of brucellosis after a 2-year disease eradication campaign that utilized test and removal. This herd originated from YNP bison in 1941 and had a peak seroprevalence rate of approximately 10% in 1961 (Nishi, 2010). Recent research has shown that the Henry Mountain bison herd represents a genetically important subpopulation of the YNP-based metapopulation. This herd meets the YNP standard of no detectable cattle introgression, but it is also free of brucellosis (Ranglack et al., 2015).
3. In 1973, the Custer State Park bison herd in South Dakota was declared free of brucellosis after a 10-year disease management program from 1963 to 1973. That herd had a peak seropositive rate of 48% in 1961. A combination of annual vaccination of calves and yearlings, test and removal, and herd size reduction were utilized (Nishi, 2010).
4. In 1974, the Wichita Mountain National Wildlife Refuge bison herd in Oklahoma went from 3% seropositive to free of brucellosis after an 11-year disease management effort. A combination of test and removal, population reduction, isolation of select groups, and vaccination of calves up until 1973 were utilized to free the herd of brucellosis (Nishi, 2010).
5. In 1985, the Wind Cave National Park bison herd in South Dakota went from a high seropositive rate of 85% in 1945 to brucellosis free after a disease management effort conducted from 1964 to 1985. A combination of whole herd and calfhood vaccination and test and removal were utilized (Nishi, 2010).
6. In 2000, a privately owned bison herd in South Dakota was released from quarantine after a 10-year effort to eliminate brucellosis from the herd. This was accomplished by a combination of testing and removal of positive animals together with herd management to reduce exposure and transmission. The main herd of older, chronically infected animals was depopulated in January 1999. Younger, uninfected animals from calf crops were separated, intensely vaccinated with RB51, tested, and retained on the ranch to rebuild the herd (USAHA, 2000).

None of the cases above, however, are comparable to the bison herds in the GYA, and those situations did not involve affected elk populations. Data are limited on the use of test and removal alone or in combination with other methods. Hobbs and colleagues (2015) forecasted the effects of annually removing 200 seropositive bison using a Bayesian model that included uncertainties associated with a number of important parameters. Removal of seropositive bison was one of the few management actions likely to reduce

Revisiting Brucellosis in the Greater Yellowstone Area

seroprevalence in the short term: from 55% to 14% over 5 years, although the credibility interval was still large, ranging from 0.12% to 57% in the fifth year (Hobbs et al., 2015).

In elk, the Muddy Creek pilot project was conducted from 2006-2010 to assess the use of test and removal to reduce prevalence of brucellosis in elk attending a Wyoming feedground. Data from that study showed that capturing nearly half of available yearling and adult female elk attending a feedground, testing for *B. abortus*, and removing those that test positive can reduce antibody prevalence of brucellosis in captured elk by more than 30% in 5 years. However, once the pilot project ended, the seroprevalence of brucellosis in elk on the feedgrounds resurged (Scurlock et al., 2010).

A variant of testing with the intention of lethal removal is test and quarantine. A bison quarantine pilot project was initiated in 2005 to determine whether it was feasible to qualify animals originating from the YNP bison herd as free from brucellosis. This project used the concept of separating seronegative, young animals so as to minimize exposure, with testing and removal. A majority of those animals were subsequently declared brucellosis-free and were moved to other locations, including to two Native American rangelands.

9. VACCINES AND DELIVERY SYSTEMS FOR CATTLE, BISON, AND ELK

Vaccination is proven to prevent or mitigate infectious diseases. A number of highly efficacious commercial vaccines exist against bacterial diseases for use in cattle, including against *Leptospira borgpetersenii* serovar Hardjo-bovis, as well as vaccines for humans, such as those against bacterial meningitis, tetanus, and *Haemophilus influenza* B. Vaccines have been shown to be an effective tool to control the spread of brucellosis when combined with management practices. Adult cattle can be safely vaccinated with conventional *Brucella* vaccines via a primary or boosting dose, and cattle may be pregnant when vaccinated. This has been shown to be efficacious and to increase the immune response as measured using in vitro tests. In wildlife, development of oral vaccination strategies would be preferable to ballistic or needle injection, and a limited number of studies have shown promise.

9.1 Improving Cattle Vaccines

Cattle vaccines to date have been designed to protect against *B. abortus*-induced abortion and not against infection. Many of the brucellosis concerns in cattle could potentially be resolved by improving cattle vaccines for resistance to infection even under high dosage challenge conditions and even when herd immunity is compromised by comingling with infected wildlife (bison and elk). In the long run, an effective vaccine to protect against infection could reduce the legal, political, and financial costs associated with brucellosis in cattle. Improvements would be needed for adult vaccines (for both primary immunizations and booster doses for previously vaccinated cattle) and therapeutic vaccines that boost or retrain immune responses of animals already infected with *Brucella* (Wright, 1942). If it were possible to develop a vaccine that would not only prevent abortion but also prevent infection in cattle, the need for wildlife vaccines may be less paramount. Comprehensive delivery of vaccines may be a particular challenge that could be avoided if cattle vaccines were sufficiently improved.

9.2 Delivery Systems for Brucellosis Vaccination of Wildlife

Vaccinating wildlife can be challenging. Vaccines have been delivered to elk by needle immunization and biobullets, but they have been ineffective. Elk are widely dispersed and mobile, and many herds—including some that are infected at a high rate—do not concentrate on accessible feedgrounds in the winter. Even if an efficacious vaccine were available for elk, vaccinating elk populations in the GYA is infeasible in the absence of a novel method for delivering the vaccine (beyond biobullets or darting). Progress toward a feasible delivery system along with developing efficacious vaccines for elk will both be critical. A recent modification of Komarov's bullets has been made and was shown to induce both antibody and cellular responses in cattle and bison with no detrimental effects (Denisov et al., 2010). While it can be delivered

Management Options

from 100 meters, the safety range is 40-60 meters which may not be feasible for all terrains found in the GYA (Denisov et al., 2010).

Oral vaccines have been suggested to better stimulate mucosal immunity because exposure to brucellosis is generally through the mucosa. The gut mucosa regularly samples antigens from the intestinal lumen via dendritic cells embedded within the epithelium or via specialized microfold cells. *Brucella* antigens are then picked up and delivered to the mucosal and systemic immune systems to stimulate anti-vaccine immunity. Thus, oral vaccines may be more effective at preventing infection than parenteral administration of the vaccine. The administration of *B. abortus* strain 19 (S19) vaccine by oral vaccination proved to be equally as effective as subcutaneous vaccination in protecting pregnant heifers from *Brucella*-induced abortion (Nicoletti and Milward, 1983; Nicoletti, 1984). Cattle have been immunized orally with *B. abortus* strain RB51 (RB51) as a model for wildlife. When RB51 was mixed with feed and fed to beef heifers, which were then bred and exposed to a challenge dose of 10^7 *B. abortus* strain 2308 organisms, it was shown that there was protection from abortion in 70% of the vaccinates but only 30% of the unvaccinated controls (Elzer et al., 1998). Microspheres composed of eggshell-precursor protein of *Fasciola hepatica* (Vitelline protein B) have been used to orally vaccinate red deer (*Cervus elaphus elaphus*) with RB51. This was shown to induce a good cellular immune response, as measured by lymphocyte proliferation assays, as well as to induce an antibody response (IgG) (Arenas-Gamboa et al., 2009b). Following challenge with another vaccine strain (S19), there was reduced bacteria in the spleens of vaccinates. A similar study using alginate microencapsulated S19 organisms to immunize red deer also showed a cellular immune response (Arenas-Gamboa et al., 2009a). Less considered is uptake of brucellae in the tonsils following exposures of the head and neck mucosa (Suraud et al., 2008). Vaccination of the tonsils may improve protection against *Brucella* infections. Thus, the development of oral and mucosal vaccination strategies for wildlife are promising.

10. STERILIZATION AND CONTRACEPTIVES

The use of sterilization and contraceptives as a tool for wildlife management is controversial. Although it cannot prevent infection, sterilizing bison or elk early in life could prevent them from breeding, becoming pregnant, and if they are also infected with brucellosis, aborting and exposing cattle or other wildlife. Surgical sterilization of cattle (spaying heifers) has been a procedure used by stockmen for years to reduce or prevent transmission of brucellosis in cattle herds. Surgically spaying wild elk and bison is infeasible, but nonsurgical reproductive control via contraception may be feasible. Contraception of bison as a potential means to slow brucellosis transmission in wildlife may be more effective than testing and removal (Ebinger et al., 2011). Ebinger and colleagues (2011) posit that in social species that form groups, sterilized individuals essentially create herd immunity similar to effective vaccination efforts. On the other hand, when seropositive individuals are removed from the population, the social group may reform and bring susceptible individuals into greater contact with the remaining infectious individuals, thereby reducing herd immunity and increasing the potential for a strong resurgence of disease (Ebinger et al., 2011).

USDA-APHIS has recently conducted research on the possible use of a gonadotropin-releasing hormone (GnRH) antagonist vaccine (GonaCon™) as a method of inducing sterility in bison and elk (Rhyan, 2015). Earlier efforts using a zona pellucida vaccine were deemed ineffective (Kirkpatrick et al., 2011). Experimental trials with GonaCon™ in elk were under way as of the writing of this report. Information provided by USDA indicated that GonaCon™ has been approved by the U.S. Environmental Protection Agency (EPA) for use in deer and wild horses (Rhyan, 2015). In most species, GonaCon™ provided 2-3 years of sterility and the animals were anestrus (did not come into breeding condition). However, 5%-15% of animals became permanently sterile (up to 5 years), adjuvants caused some injection site reactions (abscesses), and protection was not 100% (Rhyan, 2015).

GonaCon™ has been better tested in bison than in elk. From 2002-2008, five vaccinated captive bison in Idaho did not calve while a small number of control bison calved 75% of the time (Rhyan, 2015). Bison that were in mid-to-late pregnancy when first vaccinated calved normally. A dose-response study showed that a high dose of GonaCon™ was 86% effective, low dose was 50% effective, and the medium dose

Revisiting Brucellosis in the Greater Yellowstone Area

between those levels (Rhyan, 2015). In field trials with free-ranging bison in southern Colorado, there were mixed results: GonaCon™ vaccinated cows had 7 calves while unvaccinated cows had 24 calves. A field trial at Corwin Springs examined rates of infection and abortion in 20 vaccinated and 20 control bison cows exposed to brucellosis, and GonaCon™ appeared to be effective at significantly reducing abortion and birthing of infected bison calves (Rhyan, 2015). Another set of trials at Corwin Springs with 15 vaccinates and 15 controls had mixed results. In the first year, 75% of controls became pregnant while 20% of vaccinates did; in the second year, 77% of controls became pregnant while only 13% of vaccinates did; in the third year, 90% of controls became pregnant but so did 36% of vaccinates (Rhyan, 2015).

No large, free-ranging wildlife population in North America has ever been successfully managed using contraception. Modeling studies for wild horses suggests that even highly effective contraceptives can at best only slow population growth (Garrott et al., 1992; Gross, 2000; Ballou et al., 2008). Contraception conjures up the notion of manipulation that may be unacceptable to the public. By decreasing reproduction, it could also be seen as decreasing future hunter harvest and potentially jeopardizing their acceptance. The management of elk inside national parks is under the jurisdiction of the NPS and outside national parks is under the authority of state wildlife management agencies. It is unclear whether state agencies or the NPS would allow experimental use of GnRH vaccines in free-ranging elk as part of brucellosis management efforts. With limited information available on GonaCon™ and other contraceptive approaches at the writing of this report, they would currently not be considered as a viable management option.

11. PREDATION AND SCAVENGERS

There are a number of mechanisms by which both scavengers and predators are likely to affect the distribution and abundance of elk as well as the transmission and prevalence of brucellosis. Scavengers and predators play a valuable role in suppressing the spread of brucellosis, as *B. abortus* is known to survive for weeks or months under typical GYA winter conditions and for up to 6 months if protected from sunlight (Stableforth, 1959). For the most part, the efficacy of predation and scavenging to alter brucellosis dynamics is unknown and untested. In the absence of healthy predator populations, however, elk may exceed management objectives, particularly in regions with limited hunter access (Haggerty and Travis, 2006; Cole et al., 2015). In this scenario, managers could consider further restricting the tag limits on predators or increasing the tag limits for elk. This would likely be a contentious decision, and it remains to be determined whether the benefits associated with fewer elk would be offset by the additional livestock losses that are likely to coincide with increasing predator populations in localized areas.

USDA-APHIS's Wildlife Services removes coyotes from many regions across the country at the request of individual landowners. Coyotes are categorized as predators and can be shot or trapped in Idaho, Montana, and Wyoming without a license. However, coyotes are a major scavenger of aborted fetuses, and they are likely to reduce transmission rates both among elk and between elk and livestock (Maichak et al., 2009). Coyote hunting is unregulated; thus, it is unknown how many coyotes are removed annually and whether restricting coyote harvest would have any beneficial effect on brucellosis transmission. Again, this management tool is likely to incur a direct trade-off for the producer in the form of additional calf losses.

Several different avenues could be explored with respect to trained dogs (Wasser et al., 2004). First, in localized areas such as winter feedlines, dogs could be used by producers to investigate an area for fetuses daily prior to bringing cattle out. Because this would create a significant risk to the dog for becoming infected with brucellosis, the dogs would need to be muzzled to prevent ingestion or be trained to find abortions in an area and to stay a safe distance away. In addition, dogs have been used in some cases to detect certain forms of cancer in humans (Cornu et al., 2011). If detection dogs could be used pen-side to detect actively infected elk, bison, or cattle, this would facilitate more targeted test-and-remove or sterilization approaches.

Management Options

REFERENCES

- Adams, G.L. 1990. *Advances in Brucellosis Research*. College Station, TX: Texas A&M University Press.
- Almberg, E.S., P.C. Cross, C.J. Johnson, D.M. Heisey, and B.J. Richards. 2011. Modeling routes of chronic wasting disease transmission: Environmental prion persistence promotes deer population decline and extinction. *PLOS ONE* 6(5):e19896.
- Arenas-Gamboa, A.M., T.A. Ficht, D.S. Davis, P.H. Elzer, M. Kahl-McDonagh, A. Wong-Gonzalez, and A.C. Rice-Ficht. 2009a. Oral vaccination with microencapsulated strain 19 vaccine confers enhanced protection against *Brucella abortus* strain 2308 challenge in red deer (*Cervus elaphus elaphus*). *Journal of Wildlife Diseases* 45(4):1021-1029.
- Arenas-Gamboa, A.M., T.A. Ficht, D.S. Davis, P.H. Elzer, A. Wong-Gonzalez, and A.C. Rice-Ficht. 2009b. Enhanced immune response of red deer (*Cervus elaphus*) to live RB51 vaccine strain using composite microspheres. *Journal of Wildlife Diseases* 45(1):165-173.
- Ballou, J.D., K. Traylor-Holzer, A.A. Turner, A.F. Malo, D. Powell, J. Maldonado, and L. Eggert. 2008. Simulation model for contraceptive management of the Assateague Island feral horse population using individual-based data. *Wildlife Research* 35:502-512.
- Brandt, A., M. W. Sanderson, B.D. DeGroot, D.U. Thomson, and L.C. Hollis. 2008. Biocontainment, biosecurity and security practices in beef feedyards. *Journal of American Veterinary Medical Association* 232:262-269.
- Brennan, A. 2015. *Landscape-scale Analysis of Livestock Brucellosis*. USDA's Animal and Plant Health Inspection Service.
- Caetano, M.C., F. Afonso, R. Ribeiro, A.P. Fonseca, D.A. Abernethy, and F. Noinas. 2016. Control of bovine brucellosis from persistently infected holdings using RB51 vaccination with test and slaughter: A comparative case report from a high incidence area in Portugal. *Transboundary and Emerging Diseases* 63:e39-e47.
- Clifford, D.L., B.A. Schumaker, T.R. Stephenson, V.C. Bleich, M.L. Cahn, B.J. Gonzales, W.M. Boyce, and J.A.K. Mazet. 2009. Assessing disease risk at the wildlife-livestock interface: A study of Sierra Nevada bighorn sheep. *Biological Conservation* 142:2558-2568.
- Coburn, D.R. 1948. Special Report of field Assignment at Yellowstone National Park, January 10-29, 1948. Yellowstone National Park, WY. 30 pp.
- Cole, E.K., A.M. Foley, J.M. Warren, B.L. Smith, S.R. Dewey, D.G. Brimeyer, W.S. Fairbanks, H. Sawyer, and P.C. Cross. 2015. Changing migratory patterns in the Jackson elk herd. *Journal of Wildlife Management* 79(6):877-886.
- Conner, M.M., M.W. Miller, M.R. Ebinger, and K.P. Burnham. 2007. A meta-BACI approach for evaluating management intervention on chronic wasting disease in mule deer. *Ecological Applications* 17(1):140-153.
- Conover, M.R. 2001. Effects of hunting and trapping on wildlife damage. *Wildlife Society Bulletin* 29(2):521-532.
- Consolo-Murphy, S. 2015. Presentation at the Second Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Moran, MT.
- Cornu, J.-N., G. Cancel-Tassin, V. Ondet, C. Girardet, and O. Cussenot. 2011. Olfactory detection of prostate cancer by dogs sniffing urine: A step forward in early diagnosis. *European Urology* 59(2):197-201.
- Creech, T., P.C. Cross, B.M. Scurlock, E.J. Maichak, J.D. Rogerson, J.C. Henningsen, and S. Creel. 2012. Effects of low-density feeding on elk-fetus contact rates on Wyoming feedgrounds. *Journal of Wildlife Management* 76(5):877-886.
- Cross, P.C., W.H. Edwards, B.M. Scurlock, E.J. Maichak, and J.D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications* 17(4):957-964.
- Cross, P.C., E.K. Cole, A.P. Dobson, W.H. Edwards, K.L. Hamlin, G. Luikart, A.D. Middleton, B.M. Scurlock, and P.J. White. 2010a. Probable causes of increasing brucellosis in free-ranging elk of the Greater Yellowstone Ecosystem. *Ecological Applications* 20(1):278-288.
- Cross, P.C., D.M. Heisey, B.M. Scurlock, W.H. Edwards, M.R. Ebinger, and A. Brennan. 2010b. Mapping brucellosis increases relative to elk density using hierarchical Bayesian models. *PLOS ONE* 5(4):e10322.
- Denisov, A.A., O.M. Karpova, Y.S. Korobovtseva, K.M. Salmakov, O.D. Sklyarov, A.I. Klimanov, M.N. Brynskykh, K.V. Shumilov, and R.V. Borovick. 2010. Development and characterization of a modified Komarov's bullet for ballistic delivery of live *Brucella abortus* strains 82 and 19 to cattle and bison. *Vaccine* 28(Suppl. 5):F23-F30.

Revisiting Brucellosis in the Greater Yellowstone Area

- Ebinger, M.R., P.C. Cross, R.L. Wallen, P.J. White, and J. Treanor. 2011. Simulating sterilization, vaccination, and test-and-remove as brucellosis control measures in bison. *Ecological Applications* 21(8):2944-2959.
- Elzer, P.H., F.M. Enright, L. Colby, S.D. Hagius, J.V. Walker, M.B. Fatemi, J.D. Kopec, V. C. Beal, Jr., and G.G. Schurig. 1998. Protection against infection and abortion induced by virulent challenge exposure after oral vaccination of cattle with *Brucella abortus* strain RB51. *American Journal of Veterinary Research* 59(12):1575-1578.
- European Commission. 2009. P. 8 in Working Document on Eradication of Bovine, Sheep and Goats Brucellosis in the EU. Available online at http://ec.europa.eu/food/animals/docs/diseases_erad_bovine_sheep_goats_brucellosis_en.pdf (accessed October 21, 2016).
- FAO (Food and Agriculture Organization of the United Nations). 2010. Good Practices for Biosecurity in the Pig Sector. Available online at <http://www.fao.org/3/a-i1435e.pdf> (accessed January 10, 2017).
- Foley, A.M., P.C. Cross, D.A. Christianson, B.M. Scurlock, and S. Creel. 2015. Influences of supplemental feeding on winter elk calf:cow ratios in the southern Greater Yellowstone Ecosystem. *Journal of Wildlife Management* 79(6):887-897.
- Forristal, V.E., S. Creel, M.L. Taper, B.M. Scurlock, and P.C. Cross. 2012. Effects of supplemental feeding and aggregation on fecal glucocorticoid metabolite concentrations in elk. *Journal of Wildlife Management* 76(4):694-702.
- Garrott, R.A., D.B. Siniff, J.R. Tester, T.C. Eagle, and E.D. Plotka. 1992. A comparison of contraceptive technologies for feral horse management. *Wildlife Society Bulletin* 20:318-326.
- Goodwin, B.K., and T.C. Schroeder. 1994. Human capital, producer education programs, and the adoption of forward-pricing methods. *American Journal of Agricultural Economics* 76(4):936-947.
- Goodwin, B.K., and V.H. Smith. 2013. What harm is done by subsidizing crop insurance? *American Journal of Agricultural Economics* 95(2):489-497.
- Grannis, J.L., J.W. Green, and M.L. Bruch. 2004. Animal health: The potential role for livestock disease insurance. *Western Economics Forum*, April 2004. Available online at <http://ageconsearch.umn.edu/bitstream/27972/1/03010001.pdf> (accessed January 10, 2017).
- Gross, J.E. 2000. A dynamic simulation model for evaluating effects of removal and contraception on genetic variation and demography of Pryor Mountain wild horses. *Biological Conservation* 96:319-330.
- Haggerty, J.H., and W.R. Travis. 2006. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 37:816-830.
- Heffelfinger, J.R. 2013. Hunting and trapping. Pp. 130-143 in *Wildlife Management and Conservation: Contemporary Principles & Practices*. P. Krausman and J. Caine, eds. Baltimore, MD: Johns Hopkins University Press.
- Hoag, D.L., D.D. Thilmany, and S.R. Koontz. 2006. Economics of livestock disease insurance—Principles, issues and worldwide cases. Pp. 1-18 in *The Economics of Livestock Disease Insurance: Concepts, Issues and International Case Studies*. S.R. Koontz, D.L. Hoag, D.D. Thilmany, J.W. Green, and J.L. Grannis, eds. Wallingford, UK: CABI.
- Hobbs, N.T., C. Geremia, J. Treanor, R. Wallen, P.J. White, M.B. Hooten, and J.C. Rhyan. 2015. State-space modeling to support management of brucellosis in the Yellowstone bison population. *Ecological Monographs* 85(4):525-556.
- Jennelle, C.S., V. Henaux, G. Wasserberg, B. Thiagarajan, R. Rolley, and M.D. Samuel. 2014. Transmission of chronic wasting disease in Wisconsin white-tailed deer: Implications for disease spread and management. *PLOS ONE* 9(3):e91043.
- Kamath, P., J. Foster, K. Drees, C. Quance, G. Luikart, N. Anderson, P. Clarke, E. Cole, W. Edwards, J. Rhyan, J. Treanor, R. Wallen, S. Robbe-Austerman, and P. Cross. 2016. Whole genome sequencing reveals brucellosis transmission dynamics among wildlife and livestock of the Greater Yellowstone ecosystem. *Nature Communications* 7:11448.
- Kirkpatrick, L.F., R.O. Lyda, and K.M. Frank. 2011. Contraceptive vaccines for wildlife: A review. *American Journal of Reproductive Immunology* 66:40-50.
- Krausman, P.R. 2013. Defining wildlife and wildlife management. Pp. 1-5 in *Wildlife Management and Conservation: Contemporary Principles & Practices*. P. Krausman, and J. Caine, eds. Baltimore: Johns Hopkins University Press.
- Lloyd-Smith, J.O., P.C. Cross, C.J. Briggs, M. Daugherty, W.M. Getz, J. Latta, M.S. Sanchez, A.B. Smith, and A. Sweil. 2005. Should we expect population thresholds for wildlife disease? *Trends in Ecology & Evolution* 20(9):511-519.

Management Options

- Lundquist, L. 2014. Yellowstone National Park rejects remote brucellosis vaccination. Bozeman daily Chronicle, January 14, 2014. Available online at http://www.bozemandailychronicle.com/news/wildlife/yellowstone-national-park-rejects-remote-brucellosis-vaccination/article_33ba0406-7d7d-11e3-84bf-001a4bcf887aa.html (accessed January 10, 2017).
- Maichak, E.J., B.M. Scurlock, J.D. Rogers on, L.L. Meadows, A.E. Barbknecht, W.H. Edwards, and P.C. Cross. 2009. Effects of management, behavior, and scavenging on risk of brucellosis transmission in elk of western Wyoming. *Journal of Wildlife Diseases* 45(2):398-410.
- Mathiason, C.K., J.G. Powers, S.J. Dahmes, D.A. Osborn, K.V. Miller, R.J. Warren, G.L. Mason, S.A. Hays, J. Hayes-Klug, D.M. Seelig, M.A. Wild, L.L. Wolfe, T.R. Spraker, M.W. Miller, C.J. Sigurdson, G.C. Telling, and E.A. Hoover. 2006. Infectious prions in the saliva and blood of deer with chronic wasting disease. *Science* 314(5796):133-136.
- McCullough, D.R. 1979. *The Georges Reserve Deer Herd: Population Ecology of a K-selected Species*. Ann Arbor, MI: University of Michigan Press.
- MDFWP (Montana Department of Fish, Wildlife & Parks). 2015. Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 1, 2015, Bozeman, MT.
- Miller, M.W., E.S. Williams, N.T. Hobbs, and L.L. Wolfe. 2004. Environmental sources of prion transmission in mule deer. *Emerging Infectious Diseases* 10(6):1003-1006.
- Nicoletti, P. 1984. Vaccination of cattle with *Brucella abortus* strain 19 administered by differing routes and doses. *Vaccine* 2:133-135.
- Nicoletti, P., and F.W. Milward. 1983. Protection by oral administration of *Brucella abortus* strain 19 against an oral challenge exposure with a pathogenic strain of *Brucella*. *American Journal of Veterinary Research* 44:1641-1643.
- Nielsen, K., and J.R. Duncan. 1990. *Animal Brucellosis*. Boca Raton, FL: CRC Press.
- Nishi, J.S. 2010. A Review of Best Practices and Principles for Bison Disease Issues : Greater Yellowstone and Wood Buffalo Areas. ABS Working Paper No. 3. Bronx, NJ: American Bison Society and Wildlife Conservation Society.
- NRC (National Research Council). 1998. *Brucellosis in the Greater Yellowstone Area*. Washington, DC: National Academy Press.
- Organ, J.F. 2013. The wildlife professional. Pp. 24-33 in *Wildlife Management and Conservation: Contemporary Principles & Practices*. P. Krausman and J. Caine, eds. Baltimore, MD: Johns Hopkins University Press.
- PAHO (Pan American Health Organization). 2001. *Zoonoses and Communicable Diseases Common to Man and Animals*. Scientific and Technical Publication No. 580. Available online at http://www.paho.org/hq/index.php?option=com_docman&task=doc_view&gid=19187&Itemid=270 (accessed January 10, 2017).
- Peck, D.E. 2010. Bovine brucellosis in the Greater Yellowstone area: An economic diagnosis. Western Economic Forum, Spring 2010. Available online at http://ageconsearch.umn.edu/bitstream/176167/2/WEF-Vol.9-No.1-Spring2010-1_Peck.pdf (accessed January 10, 2017).
- Pennings, J.M.E., and P. Garcia. 2001. Measuring producers' risk preferences: A global risk-attitude construct. *American Journal of Agricultural Economics* 83(4):993-1009.
- Pérez-Sancho, M., T. García-Seco, L. Domínguez, and J. Álvarez. 2015. Control of animal brucellosis—The most effective tool to prevent human brucellosis. Pp. 201-246 in *Updates on Brucellosis*. M.M. Baddour, ed. In Tech. Available online at <http://cdn.intechopen.com/pdfs-wm/49083.pdf> (accessed January 10, 2017).
- Proffitt, K.M., N. Anderson, P. Lukacs, M.M. Riordan, J.A. Gude, and J. Shamhart. 2015. Effects of elk density on elk aggregation patterns and exposure to brucellosis. *Journal of Wildlife Management* 79(3):373-383.
- Ranglack, D.H., L.K. Dobson, J.T. du Toit, and J. Derr. 2015. Genetic analysis of the Henry Mountains Bison Herd. *PLOS ONE* 10(12):e0144239.
- Reeling, C.J., and R.D. Horan. 2014. Self-protection, strategic interactions, and relative endogeneity of disease risks. *American Journal of Agricultural Economics* 97(2):452-468.
- Rhyan, J. 2015. USDA APHIS Brucellosis Research Efforts. Presentation at the Third Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Jackson Lake Lodge, WY.
- Rice, E. 2015. Impact of Brucellosis on Montana Livestock Production. Presentation at the First Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, July 2, 2015, Bozeman, MT.
- Rimbey, N., and L.A. Toreel. 2011. *Grazing Costs: What's the Current Situation?* Agricultural Economics Extension Series No 2011-02, March 22, 2011. Moscow, ID: University of Idaho. Available online at <http://web.cals.uidaho.edu/idaohagbiz/files/2013/01/GrazingCost2011.pdf> (accessed May 26, 2017).
- Roberts, T.W., D.E. Peck, and J.P. Ritten. 2012. Cattle producers' economic incentives for preventing bovine brucellosis under uncertainty. *Preventive Veterinary Medicine* 3:187-203.

Revisiting Brucellosis in the Greater Yellowstone Area

- Scurlock, B.M., W.H. Edwards, T. Cornish, and L. Meadows. 2010. Using Test and Slaughter to Reduce Prevalence of Brucellosis in Elk Attending Feedgrounds in the Pinedale Elk Herd Unit of Wyoming; Results of a 5 Year Pilot Program. Available online at https://wgfd.wyo.gov/WGFD/media/content/PDF/Wildlife/TR_REPORT_2010_FINAL.pdf (accessed January 10, 2017).
- Smith, B.L. 2001. Winter feeding of elk in western North America. *Journal of Wildlife Management* 65(2):173-190.
- Smith, B.L. 2013. Winter elk feeding = disease facilitation. *Wildlife Professional Winter* 2013:42-47.
- Smith, B.L., and S.H. Anderson. 1998. Juvenile survival and population regulation of the Jackson Elk Herd. *Journal of Wildlife Management* 62(3):1036-1045.
- Sorensen, A., F.M. van Beest, and R.K. Brook. 2014. Impacts of wildlife baiting and supplemental feeding on infectious disease transmission risk: A synthesis of knowledge. *Preventive Veterinary Medicine* 113(4):356-363.
- Stableforth, A.W. 1959. Brucellosis. Pp. 53-159 in *Infectious Disease of Wild Animals*, Vol. 1. Diseases Due to Bacteria. A.W. Stableforth and I.A. Galloway, eds. New York: Academic Press.
- Surau, V., I. Jacques, M. Olivier, and L.A. Guilloteau. 2008. Acute infection by conjunctival route with *Brucella melitensis* induces IgG+ cells and IFN-gamma producing cells in peripheral and mucosal lymph nodes in sheep. *Microbes and Infection* 10:1370-1378.
- USAHA (U.S. Animal Health Association). 2000. Report of the Committee on Brucellosis. Pp. 191-192 in U.S. Animal Health Association Proceedings from the 104th Annual Meeting October 19-26, 2000, Birmingham, AL. Richmond, VA: Pat Campbell and Associates.
- USAHA. 2012. Report of the Committee on Brucellosis, October 22, 2012. Available online at <https://www.usaha.org/upload/Committee/Brucellosis/report-bru-2012.pdf> (accessed November 20, 2012).
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2009. A Concept Paper for a New Direction for the Bovine Brucellosis Program. Available online at https://www.avma.org/Advocacy/National/Federal/Documents/0912_concept_paper_for_bovine_br_program_aphis-2009-0006-0002.pdf (accessed June 4, 2016).
- USDA-APHIS. 2016. Conditions for Payment of Highly Pathogenic Avian Influenza Indemnity Claims, February 6, 2016. Available online at <http://www.regulations.gov/#!documentDetail;D=APHIS-2015-0061-0001> (accessed May 26, 2017).
- USDA-NASS (U.S. Department of Agriculture's National Agricultural Statistics Service). 2010. Agricultural Statistics. Available online at https://www.nass.usda.gov/Publications/Ag_Statistics/2010/2010.pdf (accessed May 26, 2017).
- USFWS (U.S. Fish & Wildlife Service). 2012. National Survey of Fishing, Hunting, and Wildlife-Associated Recreation. U.S. Department of the Interior, U.S. Fish & Wildlife Service, and U.S. Department of Commerce, U.S. Census Bureau. Available online at <http://www.census.gov/prod/2012pubs/fhw11-nat.pdf> (accessed January 10, 2017).
- Wasser, S.K., B. Davenport, E.R. Ramage, K.E. Hunt, M. Parker, C. Clarke, and G. Stenhouse. 2004. Scat detection dogs in wildlife research and management: Application to grizzly and black bears in the Yellowhead Ecosystem, Alberta, Canada. *Canadian Journal of Zoology* 82(3):475-492.
- Wasserberg, G., E.E. Osnas, R.E. Rolley, and M.D. Samuel. 2009. Host culling as an adaptive management tool for chronic wasting disease in white-tailed deer: A modelling study. *Journal of Applied Ecology* 46(2):457-466.
- WGFD (Wyoming Game & Fish Department). 2008a. Jackson Bison Herd Brucellosis Management Action Plan. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed January 11, 2017).
- WGFD. 2008b. Brucellosis Management Action Plan for Bison Using the Absaroka Management Area. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed January 11, 2017).
- WGFD. 2010. Annual Report. Available online at https://wgfd.wyo.gov/WGFD/media/content/PDF/About%20Us/Commission/WGFD_ANNUALREPORT_2010.pdf (accessed January 10, 2017).
- WGFD. 2011. Jackson Elk Herd Unit Brucellosis Management Action Plan Update. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed January 10, 2017).
- WGFD. 2012. Cody Elk Herd Unit Brucellosis Management Action Plan. Available online at <https://wgfd.wyo.gov/Wildlife-in-Wyoming/More-Wildlife/Wildlife-Disease/Brucellosis/Brucellosis-Reports> (accessed January 10, 2017).
- WGFD. 2015. Presentation at the Second Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, September 15, 2015, Moran, WY.
- Williams, E.S. 2005. Chronic wasting disease. *Veterinary Pathology* 42(5):530-549.

Management Options

- Williams, E.S., and S. Young. 1980. Chronic wasting disease of captive mule deer—spongiform encephalopathy. *Journal of Wildlife Diseases* 16(1):89-98.
- Wolf, C., and N. Widmar. 2014. Adoption of milk and feed forward pricing methods by dairy farmers. *Journal of Agricultural and Applied Economics* 46(4):527-541.
- Wright, A.E. 1942. Report of the co-operative bovine brucellosis work in the United States. *Proceedings of the U.S. Livestock Sanitary Association* 47:149-154.

8

Economic Issues in Managing Brucellosis**1. INTRODUCTION**

Brucellosis in the Greater Yellowstone Area (GYA) is not only a disease problem but also a complex social and economic problem. The disease is costly as it diminishes economic values associated with ranching, tourism, and related outdoor activities such as wildlife viewing and hunting, in addition to broader concerns about conservation. These costs may dramatically increase if brucellosis spreads beyond the GYA, particularly if infected cattle were moved to new, high-risk areas. There is a collective desire to address brucellosis, but managing it has been challenging as it involves allocating money among various costly management options that produce uncertain benefits accruing over a long time frame. Further complicating matters is the number of individuals, stakeholders, and agencies with authorities over various aspects of the problem and the fact that the benefits of management may not accrue to those incurring the cost (e.g., cattle producers in Kansas may benefit from reduced risks of infected GYA cattle exports). Moreover, costs and benefits can vary considerably and spatially across the various stakeholder groups (e.g., costs and benefits may differ in Montana and Wyoming). These and other social concerns around brucellosis can be addressed by using economics to examine the issues, as economics is a decision science that can be used to assess costs and benefits, help determine socially and politically desirable strategies, and assist in designing policies that incentivize individuals for taking part in the desired strategy. However, economic analysis for the GYA requires a coupled-systems approach in which values are derived from models of ecological-socio-economic interactions. This is because disease-control activities are investments that alter ecological and disease dynamics to produce benefits, perhaps in conjunction with some costs, that accrue over time. Accordingly, disease ecology plays a key role in determining economic outcomes. Human behavior also matters, as the actions of individuals and resource managers related to managing risks will affect economic outcomes and may further impact the disease ecology of the system.

The appropriate tool for assessing the short- and long-term economic and ecological impacts of managing brucellosis in the GYA is bioeconomic analysis.¹ Bioeconomic analysis uses cost-benefit analysis and predictive modeling for coupled ecological and socioeconomic systems (Clark, 2005). A simple bioeconomic cost-benefit analysis would assess the economic impact of particular disease management strategies on public and/or private lands. A more sophisticated approach, however, is using the bioeconomic framework as a decision model to identify strategies—and policies that can effectively implement those strategies—that put society's scarce economic resources to their most valued (e.g., socially or politically) uses across the GYA. Bioeconomic analysis has not yet been applied for brucellosis in the GYA, and so it is not yet possible to comment on the cost-effectiveness of various management options. Even conducting a simple cost-benefit analysis for one or more management options would be a major research undertaking

¹Bioeconomic analysis has been used to examine coupled systems management since the 1950s (Gordon, 1954; Clark, 2005), focusing initially on fisheries problems where it was used to develop individual tradeable quota (ITQ) and other rights-based markets that have seen increasing use since the 1970s (Costello et al., 2008). Bioeconomic analysis has since expanded to the management and valuation of other natural systems (Fenichel et al., 2016). The approach has recently been applied to address wildlife and livestock disease problems (e.g., Bicknell et al., 1999; Mahul and Gohin, 1999; Horan and Wolf, 2005; Fenichel and Horan, 2007a,b; Horan et al., 2008, 2010; MacLachlan et al., 2017) as well as the more general problem of invasive species management (e.g., Leung et al., 2002).

Economic Issues in Managing Brucellosis

at the present time due to the need to model a complex, coupled system for which much socioeconomic data are currently lacking; thus, it was beyond the committee's task to conduct such an analysis.

This chapter describes how bioeconomic analysis can serve as a critical decision-making framework for the adaptive management of brucellosis in the GYA, provides relevant insights from related work, and identifies gaps in knowledge that need to be filled to perform an analysis. The remainder of the chapter is divided into three major sections: Section 2 presents the framework for bioeconomic analysis, with a discussion of both economic costs and benefits (subsection 2.1) and criteria for making decisions (subsection 2.2); Section 3 examines economic efficiency in a complex system like the GYA, with discussion of the economic considerations associated with various risk mitigation and adaptation strategies; and Section 4 discusses economic values in developing appropriate brucellosis control policies in the GYA.

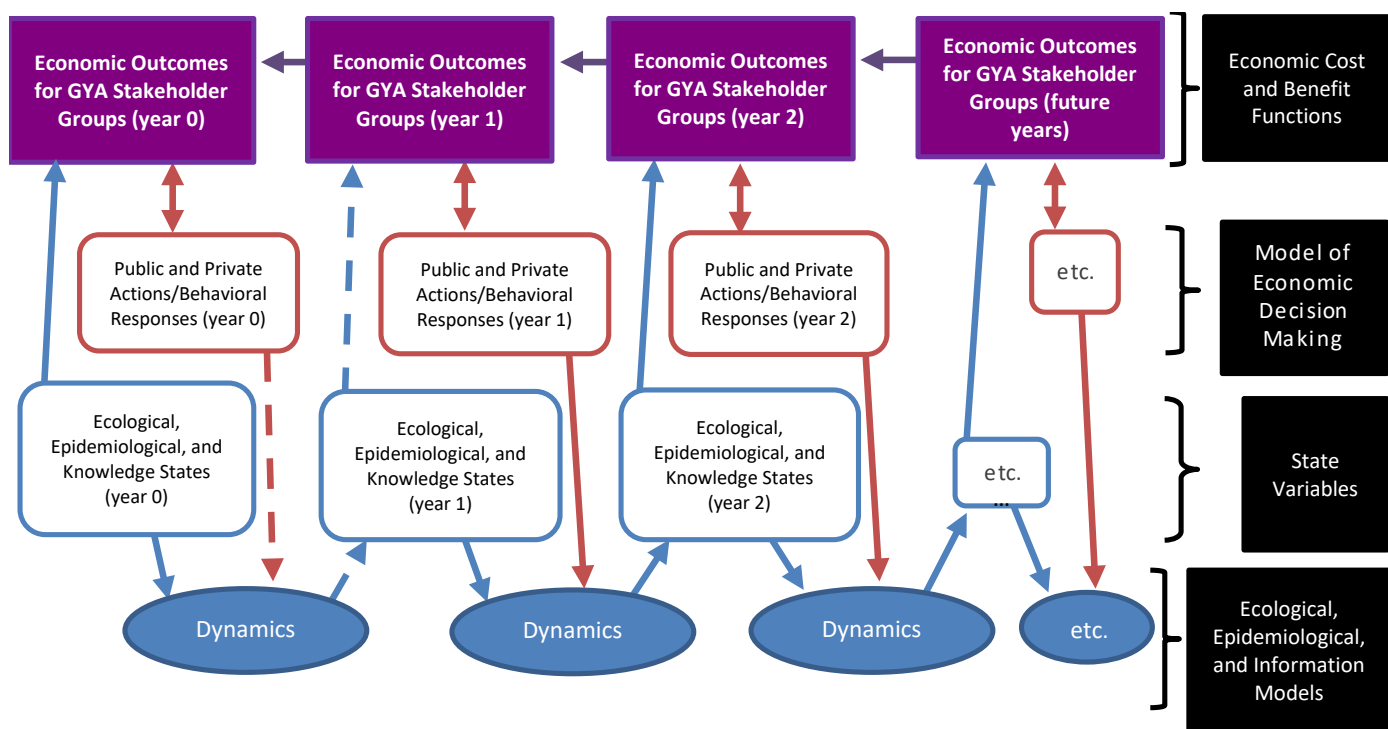
2. BIOECONOMIC FRAMEWORK

A bioeconomic framework, illustrated in Figure 8-1, involves integrating two types of models. First is a disease ecology model of population growth and disease transmission for a wildlife-livestock system that incorporates the impacts of human actions. This model is commonly based on an *S-I-R*-type model (susceptible, infected, recovered) that divides the relevant animal populations into interacting sub-populations according to disease status (Anderson and May, 1979) and is modified to account for the impact of human choices on population and infection dynamics (e.g., Fenichel et al., 2011). Recent approaches employ Bayesian state-space models to address disease ecology uncertainties (Springborn and Sanchirico, 2013; Hobbs et al., 2015; MacLachlan et al., 2017), including unobservable states and uncertainty about the effectiveness of human efforts to interrupt disease transmission or to affect other variables such as mortality and reproduction.

Second is an economic model that incorporates human responses to ecological changes for predicting economic impacts over time. This model consists of two components: economic cost and benefit functions, and an economic model of decision making. The first component is a set of economic cost and benefit functions that indicates how various costs and benefits depend on public and private actions, as well as on the likely current and future values of various ecological state variables (i.e., ecological variables that change over time, such as elk populations and prevalence rates). Cost and benefit functions, rather than observed past cost and benefit values, are necessary to predict future outcomes due to the investment nature of disease management. Costs and benefits may be affected by numerous uncertainties such as the effectiveness of prevention activities as well as the magnitudes of ecological variables (broadly defined to include wildlife and livestock variables) and their dynamics. These uncertainties can change over time as learning occurs. The second component is an economic model of decision making (e.g., by ranchers, hunters, and resource managers) that indicates how actions are chosen in response to current and predicted future ecological states, knowledge states, and the choices of other decision makers (e.g., regulators). The modeling of behavioral responses is important because economic outcomes ultimately depend on public and private choices in conjunction with ecological and knowledge outcomes; analyses that ignore behavioral responses can yield inaccurate results (Finnoff et al., 2005). The two economic model components—cost and benefit functions and decision-making processes—are discussed separately within the context of the GYA.

2.1 Economic Cost and Benefit Functions

Brucellosis and managing it in the GYA are likely to affect many socioeconomic cost and benefit values. The two main classes of values are market values that are generated via market transactions (e.g., ranching production costs and sales; hunting-related expenditures; tourism expenditures; elk feed costs), and nonmarket values, which arise outside of traditional markets (e.g., values for species conservation, and bequest and other cultural values; Ready and Navrud, 2002; Freeman, 2003; Mazzanti, 2003).



- Current (year 0) actions can have immediate effects on economic values, as indicated by the solid arrow to economic outcomes in year 0, and they can have delayed effects on economic values via their impacts on dynamic processes affecting future states. The delayed effects over a single period are illustrated by the dashed arrows running through year 1 states and on to economic values in year 1. While not illustrated explicitly, the effects on the year 1 states means the economic influence of current actions will persist over additional periods.
- The expected economic welfare arising from decisions made in one period takes into account economic impacts in future periods, as indicated by the horizontal arrows. Some stakeholder groups make decisions based on current economic outcomes, whereas other groups may make decisions based on the expected present value of economic outcomes.
- Uncertainties may arise throughout the system (i.e., economic values, behavioral responses, dynamic relations, and states). Modeling estimates can be updated in each period in response to new and better information.

FIGURE 8-1 A bioeconomic assessment of economic costs and benefits.

Economic Issues in Managing Brucellosis

Nonmarket values may seem less tangible, but they nonetheless represent real, quantifiable economic values that are regularly used to inform policy (Freeman, 1993, 2003; NRC, 2004).² These values may reflect various social issues bearing on decision making, to the extent that these social issues impact positively or negatively on the well-being of individuals with an interest in the GYA.

Both market and nonmarket values stem from how the provision of some good or service affects well-being. Impacts to well-being can be measured in different ways, but having a common metric facilitates comparisons of different impacts. There are several advantages to using a monetary metric. One is that individuals and policy makers are accustomed to evaluating decisions based on monetary values. Another is that many impacts to well-being are already monetized through individuals' choices in market transactions. Nonmarket impacts are implicitly monetized in situations where individuals evaluate monetary and nonmonetary trade-offs to determine whether a noneconomic impact is worth the economic impact (Freeman, 1993). For instance, when deciding whether to sell the family ranch, a rancher will need to determine whether there will be a direct economic gain (i.e., the offer price exceeds the present value of future profits) and then whether this gain exceeds the loss of nonmarket values (e.g., bequest or heritage values) associated with giving up the ranching lifestyle and the opportunity to pass the ranch to descendants.

There are key market and nonmarket costs and benefits that accrue annually to determine the economic welfare of several important GYA stakeholder groups.³ The investment nature of disease management means the appropriate economic welfare measure for each group accounts for the expected stream of net benefits accruing over time (e.g., an expected net present value). A cost-benefit analysis requires predicting future economic impacts by predicting changes in ecological states and behavioral responses to these changes (Clark, 2005; Finnoff et al., 2005). This means the coupled nature of the system—the manner in which behavior affects and is affected by ecological variables—plays a key role in determining economic impacts. Uncertainty also plays a key role for predicting future impacts. Additional costs arise when individuals are risk-averse, as uncertainty is costly.⁴ Note that the probability of disease transmission from elk, bison, or cattle herds likely depends on the distribution of these herds across the landscape, so that welfare measures depend on ecological variables.

Ranchers' Values

The GYA ranching community, as well as non-GYA ranchers at risk of infection via GYA cattle exports or wildlife migration, benefits from the business of cattle production: from running outfitting businesses (which includes selling access to their land for hunting and wildlife viewing), and from nonmarket benefits such as the overall enjoyment of their land under various uses (amenity values), wildlife conservation, and the ability to continue ranching over multiple generations (bequest or heritage values) (Schumaker et al., 2012). Ranchers' economic welfare for any given time period is calculated as producers' profits from market activities (revenues less costs associated with production and disease management; Just et al., 2005) plus the ranchers' nonmarket values. These nonmarket values may have ecological linkages, as ranchers may consider infection risks from wildlife when making risk-management decisions and because wildlife abundance affects the demand for hunting and wildlife viewing on their lands.

²Examples of how nonmarket valuation is used in practice include the following: by the U.S. Environmental Protection Agency to analyze the benefits of numerous environmental programs (particularly to perform cost-benefit analysis under the Clean Air Act); by various state fisheries and wildlife departments to determine recreational fishing and hunting demand for use in improving management; and for natural damage assessment and associated litigation (e.g., the *Exxon Valdez* and BP oil spills). See McCollum (2003) for a number of specific examples.

³This discussion is not exhaustive, as research on economic cost and benefit functions for the GYA is limited.

⁴Further analysis is necessary in such cases to estimate ranchers' risk preferences over uncertain outcomes to accurately measure both costs as well as any cost-mitigating behaviors.

Revisiting Brucellosis in the Greater Yellowstone Area

The economic cost of brucellosis that is incurred in a given period by GYA ranchers, as well as by non-GYA ranchers with at-risk herds, is the reduction in economic welfare to these ranchers relative to the risk-free outcome. In other words, the costs are reduced profits and nonmarket values. Reductions in profits may stem from reduced productivity on infected ranches reduced market values of goods and services produced on ranches within brucellosis-infected regions due to consumers' concerns about infection and increased costs due to risk mitigation (actions to reduce the likelihood of cattle infections) and adaptation (actions to reduce economic impacts after infection occurs) (Perrings, 2005).

Brucellosis management policies can reduce ranchers' disease-related costs, with the policies implemented in one period reducing these costs over many time periods due to the investment nature of brucellosis management. Accordingly, the net benefits of brucellosis management policies are the expected present value of increased economic welfare relative to the case of no intervention.⁵

Producers' profit functions are needed to predict disease-related costs or management-related benefits. For various GYA localities, these functions can be estimated econometrically as functions of cattle inventories, herd and disease management activities, and infection risks that depend on wildlife densities.⁶ These estimates would be based on reported activity levels, farm inventories, revenue and cost data, and data on disease risks from wildlife. The U.S. Department of Agriculture's National Agricultural Statistics Service (USDA-NASS) collects some data and reports values that are aggregated over farms (to maintain rancher confidentiality) and by certain classes of expenditures (e.g., labor, machinery). But these data do not parse out specific risk-management activities, nor do they or any other data source report on outfitting operations. Ranchers would have to be surveyed to obtain this information. Ranchers were surveyed to estimate the costs of implementing various risk-management practices on an average farm in the southern GYA (Roberts et al., 2012). These risk-management practices include hazing of elk, fencing haystacks, spaying heifer calves, adult cattle booster vaccination, modified winter feeding schedules for cattle, riding through cattle herds to prevent cattle-elk contacts, and delaying grazing on public lands; however, the effectiveness of these practices—along with the associated benefits to ranchers and society—remains highly uncertain (Roberts et al., 2012).

The USDA-NASS data may not provide enough information about price variability in response to spatial infection risks, although this information would be important to perform a cost-benefit analysis. Surveys of ranchers, combined with data on spatial transmission risks from wildlife, might facilitate estimation of these consumer-driven price responses.

Benefit functions for nonmarket goods and services valued by ranchers (e.g., amenities and bequests) are also needed to predict disease-related costs or management-related benefits. These functions can be estimated using stated preference methods that either survey individuals about their values (contingent valuation methods) (Boyle, 2003) or estimate values based on hypothetical choices made by individuals in experimental conditions (attribute-based methods involving choice experiments) (Adamowicz et al., 1998; Holmes and Adamowicz, 2003). Ecological linkages may be important. For instance, amenity and conservation benefits at any point in time likely depend on the current distribution of wildlife herds across the landscape; thus, the surveys or experiments used to elicit the benefit functions will need to account for this ecological linkage. The committee is not aware of such studies for the GYA.

⁵The term “net benefits” is used because brucellosis management policies may impose some regulatory costs on ranchers. Depending on the specific policy, these costs may include increased rancher expenditures, reduced productivity, or impacts to market values. Regulatory costs, which are generated by specific policy choices rather than the disease itself, are distinct from brucellosis costs.

⁶When estimation is based on observed or reported production and risk management behaviors, estimation generally involves making assumptions about the decision-making processes (e.g., maximizing expected profits or utility) that led to these behaviors (Greene, 2017). Hence, economic behavior and also ecological variables, to the extent that behavior depends on these, will play a role in estimation. Also, profits associated with jointly produced activities will need to be jointly estimated. For instance, land uses and risk mitigation practices such as wildlife hazing jointly affect the profitability of both ranching and outfitting activities; see Chambers (1988) for more on the economics of joint production systems.

Economic Issues in Managing Brucellosis

Market impacts associated with ranching and outfitting go beyond ranchers. As brucellosis risks alter ranchers' demands for various production inputs (e.g., feed, grazing on public lands, machinery, veterinary services), there will be additional short- and long-run economic effects in related sectors as well as in local economies where ranchers spend their income. Furthermore, brucellosis and its management may adversely impact the provision of outfitting services and hence consumers of these services (e.g., hunters or wildlife viewers).

Hunters' Values

Hunting may occur in outfitting markets involving access payments to landowners or outside of markets where such fees do not arise (e.g., on public lands). In either case, economic net benefits to hunters are defined as the willingness to pay for hunting less hunting-related expenditures (e.g., travel, access payments, permits, and equipment) and the opportunity cost of leisure. Hunter benefits can be calculated based on the demand for hunting trips. This demand can be estimated using random utility models that are based on actual trip behavior (a revealed preference approach) (Freeman, 1993; Parsons, 2003). Estimates are produced spatially and can indicate how behavior is responsive to changes in ecological states. The demand for hunting trips may also be estimated from surveys that ask hunters where they might visit, rather than where they did visit, under different scenarios (a stated preference approach) (NRC, 2004).

Instead of estimating the demand for hunter visits, which does not link to harvesting directly, Kauffman and colleagues (2012) estimate hunter demand for elk permits in northwest Wyoming. This framework is more applicable to a bioeconomic analysis involving harvesting behavior (Fenichel et al., 2016). Kauffman and colleagues (2012) model this demand as a function of elk and wolf populations, and hunter success—which in turn is estimated as a function of elk numbers—and found a link between elk population and demand that could have significant economic impacts. For instance, they found that a 50% reduction in seven elk herds with access to feedgrounds may reduce regional expenditures (not economic welfare) associated with elk hunting by more than \$500,000 per year (Kauffman et al., 2012). This finding indicates a potential economic trade-off between the benefits of disease management and hunting.

Wildlife Viewers' and Conservationists' Values

Economic benefit functions for wildlife viewing can also be modeled based on the demand for trips. Loomis and Caughlan (2004a,b) used a stated preference approach to examine the relation between elk and bison numbers in the National Elk Refuge (NER) and the Grand Teton National Park (GTNP) and tourism to these locations and the associated economic outcomes (with no consideration of disease impacts). Their approach did not facilitate estimation of a tourism benefit function that depends on elk and bison numbers, which is required for a bioeconomic analysis. However, their results do indicate a potentially large economic trade-off between the benefits of disease management and wildlife viewing.⁷

Conservationists (including landowners, hunters, and tourists) may have nonmarket values that depend on wildlife stocks: for instance, values for wildlife populations that are at healthy abundance levels and safe from disease, or values associated with using predators to control populations. Wolves serve as a predator control for elk and positively influence visitation to Yellowstone National Park (YNP), thereby

⁷Loomis and Caughlan (2004a,b) estimate how several discrete management scenarios might alter visitation choices by GTNP tourists and how this would impact income (not the social net benefits of tourism) to the local economy. For instance, under management conditions at the time of that study, (nonlocal) tourism-related income was estimated at \$306.5 million. Under a scenario involving reduced elk feeding and hunting regulations that may reduce elk populations by nearly 28% and bison populations by nearly 42%, tourism-related income may be reduced by \$23.3 million due to less tourism. Under a scenario of no active management (no feeding, no limit on hunters) that would reduce elk populations by nearly 71% and reduce bison populations by nearly 67%, tourism-related income would fall by \$62.2 million.

Revisiting Brucellosis in the Greater Yellowstone Area

generating economic value (Duffield et al., 2006).⁸ Conservationists may also have nonmarket values that depend on certain activities, such as negative values (costs) associated with the number of animals vaccinated using biobullets (which are no longer used), the number of animals culled inside national parks, the number of animals whose migration is limited by human intervention, and the amount of supplemental feeding that occurs. Many of these latter values may reflect a preference that wildlife populations remain “wild” in the NER and GTNP (Loomis and Caughlin, 2004a). Also, other things being equal, marginal values of these costs and benefits might be larger for bison, which are considered a symbol of the American west. The sorts of “non-use” values described are stated preference methods.

The Public Sector’s Values

Local, state, and federal agencies are stakeholders that incur costs from program expenditures and also benefit from generating revenues (e.g., hunting fees) to fund other programs. The social cost for the public sector to manage elk (test and removal, low-density feeding, and strain 19 vaccination) may exceed public expenditures on risk management due to transaction costs and the opportunity cost of reallocating resources from other valued programs (Alston and Hurd, 1990; Boroff et al., 2016).

Values of Ecosystem Services and of Learning

The nonmarket values previously described do not include any values associated with dynamic ecosystem processes and learning. Pertinent ecosystem processes would include valuable services such as the reproduction of healthy wildlife, as well as costly disservices such as disease transmission. These services are generally not valued directly, but instead have value because they affect the longer-run production of other goods and services that have value. For instance, hunters and conservationists generally do not directly value wildlife reproduction that produces healthy offspring; they value the future use and enjoyment of these offspring. People also do not place a negative value directly on disease transmission, but rather a negative value is placed on the adverse future outcomes from having more infected animals.

Ecosystem values are calculated as part of bioeconomic analysis, and these values play an important role in determining the values associated with various management activities (Barbier, 2000).⁹ Activities that enhance reproduction of healthy animals are an investment in a valued natural asset (healthy wildlife) that produces returns accruing in multiple future periods (benefits of future conservation, wildlife viewing, and harvesting). Activities that manipulate the natural system to produce valuable information for future management represent a valuable investment in knowledge assets. Activities that enhance disease transmission are an investment in a costly natural liability (infected animals) that produces losses accruing in multiple future periods (losses from infected cattle and welfare losses to conservationists). Alternatively, actions to reduce transmission are beneficial investments in reducing disease liabilities. The perspective that actions affecting ecological and information (knowledge) dynamics represent investments in future economic impacts facilitates the calculation of the longer-term costs and benefits of an action and also makes it possible to attribute these values to the relevant stakeholder groups.

Many disease-control actions do not only affect transmission; they may also adversely affect valuable resource assets in addition to reducing disease liabilities, generating costs in addition to disease-control benefits. For instance, harvesting wildlife non-selectively (i.e., irrespective of disease status) removes healthy animals so that they are unavailable for future use or enjoyment by humans or for reproduction, and it removes diseased animals so that they are unavailable for generating future disease costs. Supplemental feeding is also non-selective, as it is not possible to only reduce feeding of infected animals. Therefore,

⁸The economic impacts reported were based on spending rather than net benefits. Economic impacts to cattle and hunters due to wolf predation are also discussed, but Duffield and colleagues (2006) acknowledge a number of uncertainties, and no formal analysis was provided.

⁹The bioeconomic approach to the valuation of ecosystem services is also referred to as the dynamic production function approach to economic valuation, which is an improvement over static approaches (Barbier, 2000).

Economic Issues in Managing Brucellosis

reduced feeding is beneficial in terms of reducing infectious contacts and increasing mortality rates of infected animals, but costly in terms of increasing mortality rates of healthy animals.

The returns or losses to ecological and knowledge investments, which vary over space and time, ultimately depend on how the populations are managed spatially over time (Barbier, 2011). This means that GYA wildlife and cattle management strategies at different points in time and space and for different purposes are not independent.

2.2 Decision-Making Criteria

The expected economic outcomes associated with disease management depend on the specific management choices. These are not merely public policy choices but the private responses to those choices. It is therefore necessary to model private and public decision-making processes to predict and analyze behavioral responses to disease risks and other economic considerations.

Economic models generally assume decisions are made to maximize some private or public measure of economic welfare. For instance, private individuals such as ranchers may be concerned about profits as well as nonmarket benefits associated with their family's quality of life and altruistic concerns about ecological and societal outcomes. But even with altruistic concerns, ranchers and other private individuals will generally be unwilling to incur significant costs for activities that benefit others. This means private individuals will have insufficient incentives to invest in activities that largely benefit others (referred to as generating positive externalities) (Baumol and Oates, 1988; Hanley et al., 1997). For instance, ranchers are unlikely to adopt many biosecurity activities because the private costs outweigh the private benefits (Roberts et al., 2012), even though the public benefits may outweigh the costs.

Given a model of how individuals make decisions in response to economic factors (including policy variables) and ecological factors, it is possible to perform a simple cost-benefit analysis that analyzes the expected welfare impacts of particular public policies. Specifically, such an analysis would involve predicting the dynamic economic and ecological feedback responses to a particular, pre-defined policy scenario in order to predict the expected short- and long-term economic impacts to the various stakeholder groups. Simple cost-benefit analyses that have been performed for the GYA generally focus on a subset of the system, such as impacts to one or few stakeholder groups, and may not fully incorporate dynamic feedback responses. Examples include analyses of discrete scenarios (in static settings) of the expected net benefits of elk management (Boroff et al., 2016) and the unintended consequences on elk hunting (Kauffman et al., 2012).¹⁰

A more sophisticated cost-benefit analysis evaluates economic-ecological trade-offs to determine the most desirable management strategies according to some socially relevant criterion. Specifically, public agencies' objectives may reflect a variety of considerations based on what the public wants, as reflected by some public preferences over the distribution of costs and benefits among various stakeholder groups (Rausser, 1982; Gardner, 1987; Mueller, 1989; Rausser and Foster, 1991).

¹⁰A break-even analysis was conducted for various discrete scenarios involving various on-farm risk-management practices. This includes hazing of elk, fencing all haystacks, spaying 100 heifer calves each year, administering adult booster vaccinations, feeding cattle only 1 day's worth of hay each day (rather than leaving 2 days' worth on the ground) in the winter, hiring a rider to prevent cattle-elk contacts by riding through cattle herds for 4 hours per day for 6 months, and delaying grazing on public lands by 1 month (Roberts et al., 2012). That study specifically determined the minimum level of practice effectiveness that makes each scenario profitable. The analysis provides insights into relative costs of various practices. However, as the break-even point yields no net benefits, the analysis does not indicate the cost-effectiveness of each scenario. The cost-effective allocation of practices would minimize the costs of attaining a particular level of risk reduction, given current densities of infected elk. Such an analysis would require abandoning the focus on discrete scenarios limits and would instead determine the optimal level of effort applied to each practice (e.g., determining the percentage of young heifers to spay, the number of days to delay grazing, the time allocated to hazing and riding through herds, etc.).

Revisiting Brucellosis in the Greater Yellowstone Area

Economic efficiency provides a benchmark in guiding public policy, as an efficient strategy is expected to allocate economic resources to the most socially valued uses based on the costs and benefits. Specifically, an efficient strategy is determined by asking whether each dollar to be invested in a particular disease control action is expected to provide net social gains. If so, then the investment would be made and the same question would be asked about the next dollar as well as for all other potential management options. Efficiency is attained when no more gains are expected to arise from investments in any action, including planned future investments. The result is that the set of actions planned to be taken now and in the future will maximize the expected present value of current and future economic net benefits to society.

Computationally, the efficient strategy can be identified using the optimization approach of stochastic dynamic programming to address dynamic considerations as well as uncertainty about the dynamic processes that generate future states (e.g., Leung et al., 2002). The approach will involve partially observable Markov process models of disease ecology when there is also uncertainty about current states (e.g., Springborn and Sanchirico, 2013; MacLachlan et al., 2017). Optimal strategies are updated as new information emerges to better quantify uncertainties. The process ideally takes learning into consideration; the expected benefits of actively perturbing the natural system to yield valuable information for improving future management are an explicit consideration when choosing among alternative actions and the levels of these actions (Grafton and Kompas, 2005; Springborn and Sanchirico, 2013). The bioeconomic approach therefore brings economics to bear on adaptive management in ways that differ from recent analyses of adaptive management for the GYA (e.g., Hobbs et al., 2015) but are still consistent with Walters' (1986) definition of active adaptive management. As efficient strategies are identified, the bio-economic approach simultaneously estimates the economic values of these actions as well as the ecological impacts, with these predictions also being updated annually.

The efficiency criterion does not directly deal with how to equitably distribute benefits across various stakeholder groups, but it does determine the level of benefits that can be distributed. Importantly, by maximizing expected net benefits to society, the efficient strategy prevents wasteful use of resources so that, in principle, more benefits can be had by all. The concept of equity is dependent on value judgments, which are often political decisions left in the realm for decision makers to decide (Just et al., 1982). However, cost-benefit analysis based on efficiency considerations can be used to inform decision makers on the equity implications of various policy approaches.¹¹

Decision criteria defined solely in terms of expected economic outcomes (e.g., efficiency or maximizing an objective that differentially weights the welfare of different stakeholder groups) give policy makers considerable flexibility in selecting a management strategy. But sometimes agencies also have ecological objectives in addition to economic objectives. For instance, brucellosis disease eradication has been a focus of the Cooperative State-Federal Brucellosis Eradication Program (USDA-APHIS, 2012) and the former Greater Yellowstone Interagency Brucellosis Committee, and it is addressed in the disease ecology literature (Roberts and Heesterbeek, 2003). While eradication is not the stated objective of the IBMP (2015), the Interagency Bison Management Plan (IBMP) does state “these management actions demonstrate a long-term commitment ... towards the eventual elimination of brucellosis in free ranging bison in Yellowstone National Park” (USDOI and USDA, 2000).

¹¹More than one set of policy tools (e.g., taxes, subsidies, regulations) are capable of promoting efficiency, with each approach generating different distributions of economic welfare among the various stakeholder groups. In theory, these distributions can be fine-tuned using non-distortionary policies (i.e., lump sum taxes or payments) that do not cause individuals to deviate from the efficient choices. However, welfare economics suggests that non-distortionary inter- and intra-generational transfers to achieve distributional objectives will not always be feasible, and it also suggests considering both efficiency and distributional effects in optimal policy design (e.g., Gardner, 1987; Stiglitz, 1987). Even so, efficiency remains a desirable benchmark from which to evaluate these other objectives, as all stakeholders can benefit when the same distributional objectives are achieved more efficiently. Because of this, the committee focuses on efficiency but notes that in some instances the economic objective may include distributional considerations.

Economic Issues in Managing Brucellosis

Efforts can be made to cost-effectively achieve eradication (i.e., achieving the ecological objective at minimum cost to society), so that both economic and ecological objectives are addressed. However, if eradication is not efficient, then pursuing this objective will waste resources relative to how it could have been spent to more efficiently manage the problem (Fenichel et al., 2010).¹² Imposing a specific ecological objective (such as eradication) that would not be satisfied under the efficient strategy implies that policy makers—and by extension, taxpayers—are willing to spend whatever will be required to achieve the ecological objective, regardless of the cost or benefit. This is akin to committing to purchase a product prior to knowing its price or its value.

3. ECONOMIC EFFICIENCY IN A DYNAMIC, COUPLED SYSTEM

A brucellosis management strategy is efficient when the expected marginal benefits and expected marginal costs of each action are equated, where costs and benefits reflect the dynamic impacts to the coupled system (Clark, 2005).¹³ It is insufficient to simply consider the disease control impacts of the alternative disease control actions; the marginal costs and benefits associated with other impacts also need to be considered. For example, elk hunting can be implemented at a cost (e.g., travel, outfitting and time costs) to reduce transmission via reduced elk densities, thereby reducing disease liabilities (a benefit); however, hunting also involves several longer-run (intertemporal) costs associated with removing an animal: the animal is no longer available for future use and enjoyment or for reproduction (an ecosystem service). As epidemiological risks differ over time and across the GYA, so do the costs and benefits of certain actions. This means the various management actions will need to be targeted across space and time. Other things being equal, it is efficient to implement more disease-control efforts in areas or across time periods with low expected marginal costs and large expected marginal benefits.

Undertaking multiple actions generally promotes an efficient reduction in risks, in part due to the principle of diminishing marginal returns. This principle indicates that as more effort is applied to a particular activity, the marginal net benefits generally diminish (Varian, 1993). For instance, hunting to reduce elk densities may initially be an efficient approach for reducing elk transmission risk due to the significant reduction in risk for each extra unit of hunting. However, as hunting efforts are expanded to further reduce risks, the additional net gains become smaller and this approach most likely becomes less attractive relative to alternative efforts such as reduced feeding. At some point, it becomes more economical to expand disease control investments to include additional activities, even if those other activities were initially less preferable. Thus, efficiency is enhanced when each additional dollar spent on disease control is applied to the activity that yields the greatest additional or marginal expected net benefits.

The epidemiological benefits from undertaking multiple actions to reduce disease transmission can be characterized by impacts to disease management thresholds, commonly used by disease ecologists to inform management (Roberts and Heesterbeek, 2003). A disease management threshold is a population threshold associated with a single management action to reduce disease prevalence. For instance, a vaccination threshold represents the minimum percentage of the herd that needs to be vaccinated to reduce prevalence (Roberts and Heesterbeek, 2003). Alternatively, a host-density threshold defines the threshold animal density that will need to be attained via harvesting before prevalence starts to decline (Heesterbeek and Roberts, 1995). It may be expensive to alter populations to satisfy a fixed threshold condition. However, disease

¹²Eradication is only efficient if the additional benefits of eliminating the last infected animal exceed the additional costs (e.g., McInerney et al., 1992). This may not be possible if there is inter-species transmission (Bicknell et al., 1999) or there are reintroduction risks (Horan and Fenichel, 2007). Perhaps recognizing this, the National Bovine Brucellosis Surveillance Plan “reflects the shift in goals from disease eradication to detection of re-emergence and demonstrating disease-free status of U.S. domestic cattle and bison herd” (USDA-APHIS, 2012, p. 21).

¹³Efficiency simply assumes that the regulatory agency places equal weights on the welfare accruing to the various stakeholder groups. Suppose instead that the agency places unequal weights on these welfare measures. In that case, marginal costs and benefits associated with each stakeholder group are simply weighted to become marginal political costs and benefits. The qualitative results described are largely unaffected by this difference, but the quantitative results would differ.

Revisiting Brucellosis in the Greater Yellowstone Area

management thresholds may not be fixed. Undertaking additional actions may make it possible to shift a threshold in a manner such that the threshold condition becomes less stringent and hence less costly to satisfy. That is, one action may be seen as an investment in reducing the threshold associated with other actions. For instance, altering supplemental feeding practices to reduce transmission risks will generally shift the vaccination and host-density thresholds so that fewer vaccination and harvesting efforts are required to reduce prevalence (Fenichel and Horan, 2007b). Thresholds associated with one ecological variable can also change over time in response to changes in other ecological variables, particularly in spatial, multispecies systems such as the GYA. For instance, current efforts to reduce brucellosis transmission within one elk herd may improve future brucellosis thresholds in neighboring elk and bison herds. This means managers can take steps now to effectively invest in reducing future threshold values (Fenichel et al., 2010). The bioeconomic approach therefore involves managing both populations and thresholds through combinations of investments based on an evaluation of the associated costs and benefits.

Just as it is efficient to target multiple actions, it is also efficient to target economic risks at multiple levels (Baumol and Oates, 1988). Economic risk, which involves both infection probabilities and the economic outcomes of infection, can be managed by targeting efforts toward risk mitigation and adaptation (Perrings, 2005). Considering wildlife to be the source of brucellosis risk to domestic cattle and bison, risk mitigation involves reducing disease transmission among wildlife and potential exposure of healthy cattle to infection. Adaptation in this setting involves reducing expected economic impacts arising once domestic animals in the disease surveillance area (DSA) become infected, which could include reducing both DSA losses and the likelihood that infected cattle are moved outside the DSA (thereby reducing expected cattle losses outside the DSA). Efficiency generally requires a combination of mitigation and adaptation efforts that are chosen based on the marginal benefits and marginal costs of each activity (Perrings, 2005).

3.1 Risk Mitigation for Wildlife Populations

Mitigating brucellosis in wildlife involves choosing which species to target and which controls to use, and these choices may vary by location and over time. The quantitative analysis required to make these choices has not yet been developed; the committee therefore proceeds with only a qualitative discussion. Elk are currently recognized as the primary source of recent brucellosis infections in cattle (USFWS and NPS, 2007). This suggests that the largest expected marginal gains might initially come from targeting elk, although this does not mean bison populations can be ignored; it would likely be efficient to direct some efforts at bison populations that generate risks.

Disease-control measures that are better targeted at reducing disease transmission tend to be more effective, yielding greater marginal benefits while also generating fewer adverse and costly ecological impacts. Examples of actions that selectively target brucellosis transmission in elk include vaccination, fetus removal, and test and removal (others are discussed elsewhere in Chapters 7 and 10). Vaccination has long been viewed as the holy grail of elk brucellosis management, but an effective vaccine for elk does not yet exist and may not exist for some time (USFW and NPS, 2007; Maichak et al., 2017). Other actions that selectively target transmission show promise, but the associated direct costs might be excessive. Removing fetuses quickly after an abortion event is likely to be costly except at areas of high animal concentration (such as feedgrounds, where this activity may represent an effective and low-cost option). Test and removal of wildlife is also potentially costly, although it would be less so in areas of high animal densities (e.g., elk feedgrounds and where bison exit YNP for the winter). The Wyoming Brucellosis Coordination Team (WBCT) (2005) recommended a pilot project targeting test-and-removal efforts to high-risk female elk, but this strategy was not adopted (USFWS and NPS, 2007; NER and USFWS, 2014). Test and removal of elk on feedgrounds was estimated to be extremely costly relative to elk vaccination and low-density feeding (Boroff et al., 2016).

Economic Issues in Managing Brucellosis

Alternative supplemental feeding practices can be adopted to reduce elk densities (low-density feeding that spreads out feed over a larger area) or to reduce the likelihood of contacting an aborted fetus (elevated feeding). These practices are targeted in the sense that they directly affect transmission without adversely affecting healthy animals. Low-density feeding costs may be of similar or slightly greater magnitude as vaccination costs (Boroff et al., 2016). However, as low-density feeding is more effective than vaccination, it is likely that low-density feeding costs less although no cost information was available for elevated feeding (Boroff et al., 2016).¹⁴

Highly targeted approaches tend to be costly. The greater the overall marginal costs of highly targeted approaches relative to the expected marginal benefits, the more desirable it may become to adopt an imperfectly targeted approach, such as reduced supplemental feeding and increased harvesting and hunting activities. These activities are imperfectly targeted because they are nonselective as they impact both infected and non-infected animals without regard to an animal's health status. Since nonselective actions adversely impact healthy animals more when prevalence is low, these measures are more likely to generate ancillary costs that go beyond the direct expenditures for these actions. These measures are also imperfectly targeted in a spatial sense, as control efforts in one area may spur herd movements that adversely affect infection risks.

Reducing Supplemental Feeding

Feedgrounds probably support a larger elk population by reducing winter mortality for elk, but they also increase disease transmission among elk by encouraging elk to congregate. Reducing supplemental feeding is therefore likely to reduce elk seroprevalence over time, thereby generating disease control benefits. However, as supplemental feeding (as well as other changes in land use) affect infected and healthy animals nonselectively, reduced feeding may adversely impact those who value larger elk populations, such as hunters and wildlife viewers. In contrast, conservationists might value reduced feeding because it implies more natural herds, even though they are of smaller magnitude.

A reduction in supplemental feeding at a particular location also has nontargeted spatial implications, as herd movement in response to reduced feeding may generate new risks. Specifically, supplemental feeding benefits ranchers by encouraging elk to stay away from ranches and susceptible cattle. This latter effect reduces disease exposure to cattle, as elk substitute one habitat (feedgrounds) for another (private ranches). Thus, a reduction in supplemental feeding poses significant short-term risk to cattle due to the potential increase in exposure as more elk move onto private ranches. But reducing supplemental feeding may create longer-term benefits of reduced transmission, stemming from fewer and less dense elk populations. The efficiency of reducing the magnitude of feeding operations depends on whether the long-term benefits outweigh the short-term costs.

Current strategies recommend continuing supplemental feeding in the near term to reduce exposure to cattle while also investing in native forage so that supplemental feeding can eventually be reduced (USFWS and NPS, 2007; NER and USFWS, 2014). Prior bioeconomic analysis on supplemental feeding in nonspatial settings has found optimal feeding levels to vary inversely to local disease risks, with periodic (not permanent) cessation of feeding for sufficiently high-risk periods (Fenichel and Horan, 2007b; Horan et al., 2008). These results imply that permanently closing all GYA feedgrounds, as some have suggested, may be inefficient.

¹⁴Boroff and colleagues (2016) conducted an analysis that compares some costs and benefits of various elk management practices on feedgrounds. However, care should be taken not to attribute any efficiency consequences to their results. That analysis is not based on a model of a dynamic coupled system, and only some costs (direct costs of the management practice) and benefits (reduced impacts to cattle producers) are considered. Moreover, the preferred strategy is not determined from a marginal analysis, but rather stems from comparing the total net benefits of several predetermined scenarios.

Revisiting Brucellosis in the Greater Yellowstone Area

Population Controls

Reducing population levels within high-prevalence herds could reduce the potential for infectious contacts with cattle simply because there would be fewer wildlife present. A sufficient reduction in density can also lower disease prevalence by reducing infectious contacts among wildlife, but only if disease transmission is density dependent—as is the case for elk but not bison. As previously discussed, non-selective population controls imply economic impacts beyond disease control.

The efficiency of population controls is increased via spatial targeting to address brucellosis transmission within high-risk populations and from these populations to cattle. For instance, spatial control may influence elk densities on public grazing areas or the number of elk seeking refuge from hunting on private lands where hunting is not allowed. The latter is a growing concern given the growth in privately owned land in the GYA (Schumaker et al., 2012). Spatial controls may also reduce the risks of disease spread. For instance, northern movement of bison out of YNP is density dependent; reducing herd density can reduce the amount of migration and the distance traveled. Elk and bison populations in YNP are managed spatially, but for reasons other than disease control (USFWS and NPR, 2007; NER and USFWS, 2014). This is despite the WBCT's recommendation that bison population controls be based on disease prevalence (WBCT, 2005).

Managing Risk Outside the Designated Surveillance Areas

An important spatial consideration is the efficient allocation of risk mitigation efforts toward managing risks within the current DSA versus preventing expansion of the DSA (e.g., by reducing elk densities along the DSA border and in neighboring areas). Prior work on invasive species management suggests that, at the margin, it may be efficient to invest more in preventing expansion than in reducing current risks (Leung et al., 2002). While quantitative analysis would be required to confirm this for the GYA, it would be useful to ask whether one more infected ranch within the current DSA is likely to be more or less costly than an infected ranch outside of the DSA. Intuition suggests that once mitigation and adaptation efforts are already in place to address risks inside the DSA, an additional infected ranch is unlikely to be as costly as a similar ranch outside the current DSA where no adaptation mechanisms are in place. This could be particularly true if a larger infected area becomes increasingly difficult to manage and significantly increases the likelihood of broader-scale trade sanctions, which is a major concern (USDA-APHIS, 2012).

Benefits Beyond Cattle Protection

Although cattle are the major concern, there are benefits to protecting other species from brucellosis. Protecting elk and bison from brucellosis could generate significant benefits to the extent that this protection enhances ecological productivity or would be valued by hunters, wildlife viewers, and conservationists (e.g., Horan and Melstrom, 2011). Reducing prevalence among bison might generate larger marginal values simply because bison are less abundant than elk and are considered an important symbol of the American west. Measures taken to protect wildlife from brucellosis may also generate benefits that go beyond the current brucellosis problem. For instance, reducing animal contact rates to reduce the spread of brucellosis may also protect against other potential diseases, such as chronic wasting disease (CWD) in elk. Efforts to improve the overall health of elk and bison herds may also make these animals more resilient to other current and future impacts (e.g., climate change and other diseases).

3.2 Risk Mitigation by Ranchers

Risk mitigation efforts are not confined to wildlife populations; efforts can also be undertaken on ranches to mitigate risks that wildlife pose to cattle. These efforts involve preventing infectious contacts from wildlife to cattle, either by reducing exposure of cattle to potentially infectious wildlife or by reducing susceptibility of cattle to infection. Efficient brucellosis mitigation on GYA ranches involves choosing

Economic Issues in Managing Brucellosis

which controls to use, recognizing that these choices may vary by location and over time. As with mitigation efforts targeted at wildlife, it will likely be efficient to adopt a suite of controls, including efforts to reduce both exposure and susceptibility (Roberts et al., 2012), and to vary these controls spatially and temporally based on risks. The quantitative analysis required to make these choices has not yet been developed; therefore, the committee provides only a qualitative discussion.

Vaccination is the only method for reducing susceptibility. Vaccines are significantly more effective in cattle than in wildlife, although they are still imperfect and a relatively costly business expense for ranchers who operate in highly competitive cattle markets. Producers will not provide booster vaccination of adult cattle unless this is subsidized (Roberts et al., 2012). But even then, existing vaccines may not be an economical first line of defense, due to the relatively high cost and limited effectiveness as compared to other approaches (Roberts et al., 2012).

Exposure of cattle to wildlife risks may be reduced by a variety of biosecurity actions, including hazing of elk, fencing haystacks, spaying heifer calves, modified winter feeding schedules for cattle, riding through cattle herds to prevent cattle-elk contacts, and delaying grazing on public lands. A break-even analysis of these practices was conducted for GYA ranches to provide insight into practices that are likely to be more expensive (Roberts et al., 2012), although care should be taken not to attribute any efficiency consequences to these results.¹⁵ Hazing of elk and fencing haystacks are likely to be the cheapest approaches, followed by vaccination and a modified winter feeding schedule (Roberts et al., 2012). In contrast, delayed grazing appears to be the most expensive approach (Roberts et al., 2012). This ranking of alternatives only includes direct expenditures. However, as some ranchers have outfitting businesses that benefit from the presence of elk, there may be additional costs associated with biosecurity practices, such as hazing and fencing haystacks, that limit elk densities on ranches.

It is inappropriate to compare one study on the costs of elk risk mitigation efforts (Boroff et al., 2016) with another study on the costs of cattle risk mitigation efforts (Roberts et al., 2012) because the actions are implemented at different scales and produce very different types of benefits. There may be reasons why actions under either approach may be desirable. For instance, mitigation efforts targeted at wildlife may protect more cattle herds than on-farm biosecurity efforts, which may only protect a single herd. On-farm biosecurity efforts have the benefit of being a more direct, and therefore potentially more effective, means of protecting cattle, and they likely result in fewer trade-offs with hunting, wildlife viewing, and conservation than measures targeting wildlife disease transmission. However, the large geographic sizes of ranches in the GYA and the large herd sizes on these ranches could reduce the efficiency of biosecurity practices (Hennessy, 2007a,b).

Risk mitigation efforts can also be undertaken on GYA ranches to reduce the risk of brucellosis spreading across GYA cattle herds, in the case that one or more herds become infected (e.g., keeping cattle separated in grazing areas and along fence lines). The committee is not aware of any economic analysis of this issue for the GYA.

It is worth emphasizing that spatially differentiated on-farm mitigation efforts are likely to be efficient because the GYA is ecologically and economically heterogeneous. For instance, ranch location may affect the efficiency of biosecurity, as epidemiological risks differ across the GYA. Also, ranch location and herd size play a role in determining grazing decisions. Larger herds will be more expensive to move long distances and are likely to be at greater risk on any given allotment than smaller herds due to more opportunities for infectious contacts with aborted fetal material. Herd size and ranch location thus factor into trade-offs involving the travel costs and risks of different grazing opportunities.

¹⁵Roberts and colleagues (2012) investigate a number of scenarios involving fixed, predetermined effort levels applied to various practices. Their break-even analysis illustrates when a producer might find a particular scenario to be worthwhile (i.e., to yield positive net benefits to the producer), which is quite different from a marginal analysis that aims to identify an efficient mix of efforts (i.e., to yield maximum net benefits to society). Their analysis is also not based on a model of a dynamic coupled system involving spatially heterogeneous risks, for which a one-size-fits-all approach is unlikely to apply.

Revisiting Brucellosis in the Greater Yellowstone Area

3.3 Risk Adaptation by Ranchers

Economic risks to the cattle sector can also be reduced via adaptation—that is, by reducing any economic losses that are likely to arise if a herd becomes infected. There can be no risk to cattle if infection does not generate economic losses. Reducing brucellosis-related costs may not only benefit the cattle industry: with fewer economic damages from brucellosis, there will be less of a need to manage brucellosis in the wild. This means the stringency of brucellosis controls for wildlife could be reduced relative to the case of no adaptation, at least for the interior of the GYA, thereby generating additional cost savings. More specifically, with fewer risks to GYA cattle, it would be relatively more efficient to target wildlife to prevent the spatial spread of the disease (i.e., prevent the expansion of the DSA) rather than protect producers in the current DSA.

Compensation schemes that reimburse ranchers for losses are *not* adaptation mechanisms. Compensation simply involves shifting the risk from one stakeholder group (ranchers) to another (the public sector, or taxpayers), while not actually reducing the level of risk facing society. Compensation programs can actually increase risks in some instances (see Chapter 7 and section 4.2 of this chapter).

One adaptation approach for reducing brucellosis-related losses is to alter the market(s) in which producers participate. Currently, the predominant cattle operation in the GYA is the cow/calf-yearling operation (Ruff et al., 2016), which involves maintaining a breeding herd that faces continual brucellosis risks. An alternative to this is a stocker operation that purchases weaned calves and grazes them before selling them to a feedlot. Stocker operations do not involve a breeding herd, and so they would be free of brucellosis risks once they have fully transitioned to the new operation. However, stocker operations are more costly to run in the DSA relative to the Midwest, putting DSA stocker operations at a competitive disadvantage. Increased costs stem from the harsh GYA climate and a comparative lack of corn, water, and other key resources more readily available in the Midwest, along with excess feedlot and slaughter capacity in the Midwest (Allen, 2014; Meatingplace, 2014). The lack of packing and processing sector infrastructure (e.g., slaughterhouses) necessary to produce finished beef products in the GYA means that large finished animals would have to be shipped far from the GYA for processing, which is more expensive than the current practice of shipping younger and lighter cattle. The construction of a local slaughterhouse facility would reduce transportation costs, but not finishing costs.

GYA ranchers would face greater financial risks under a stocker operation, but these could be offset by reduced brucellosis risks (Ruff et al., 2014, 2016). Ranchers with a sufficiently large rate of time preference, or discount rate, might find it privately optimal to switch to a stocker operation (Ruff et al., 2014, 2016), but this only takes private market costs and benefits into account. Private nonmarket values are also relevant and could impact the decision in either direction.¹⁶ If external social benefits of reduced brucellosis risk are also taken into account, then it might be efficient for many producers to switch to a stocker operation. In this case, such a transition might have to be incentivized via subsidy.

For some locations, it also makes sense to consider an alternative land use that does not involve cattle. The land use with the greatest expected social net benefits (taking into consideration any nonmarket values for ranchers to remain in the cattle industry) ought to be encouraged, perhaps through an incentive program. In any case, it would not be surprising for a quantitative analysis to indicate that having fewer cow/calf operations is likely to be efficient. This type of finding is broadly applicable to environmental risk-management problems (Baumol and Oates, 1988).

Another proposed way to alter the market(s) in which producers participate would be to develop local markets that would pay a premium for GYA beef. Such an approach is seen as a way of increasing profitability and enabling traditional cattle operations to stay within the GYA. Research on locational branding (Tonsor et al., 2013) finds that U.S. consumers may be unwilling to pay extra for beef produced in the United States relative to other parts of North America, but it is unknown whether visitors to the GYA might be willing to pay more for GYA beef. An alternative branding option might be to promote local beef as

¹⁶For instance, altruistic/conservationist values could lead ranchers to switch to a stocker operation in order to help reduce brucellosis risks, whereas heritage values might have the opposite effect.

Economic Issues in Managing Brucellosis

improving GYA sustainability. Regardless of how branding might be developed, it is unclear whether local demand would be sufficient to support GYA producers.

A second approach to reducing brucellosis-related losses is to ensure that cattle markets do not overly penalize non-infected GYA herds when one or a few GYA herds become infected. For instance, there have been recent calls elsewhere for relaxing costly trade restrictions in response to infectious livestock disease while adopting scientifically sound risk-management approaches (ECCFMD, 2011; MDARD, 2011; DEFRA, 2014). One potentially efficient approach is to improve signaling about herd health—beyond individual testing—to facilitate trade while reducing movement risks (Hennessy et al., 2005; Horan et al., 2015). Specifically, the concept of “risk-based trading” alerts importers of the exporting herd’s health history and enables livestock trades within endemic areas, which would spur private risk-management actions by buyers and sellers (DEFRA, 2014). The European Union’s Progressive Control Pathway suggests a similar approach, including targeted movement controls that depend on how risks differ (probabilities of transmission; economic consequences of transmission) between and within infected areas where movement might occur (ECCFMD, 2011).

3.4 Mitigating Risks to Importers of GYA Cattle

Risk mitigation and adaptation efforts can also be implemented by importers of GYA cattle. For instance, risks to importers may be reduced by informing importers of herds’ health histories, testing animals prior to movement, requiring post-movement quarantines of animals from high-risk areas, and restricting animal movements from certain high-risk areas. Current DSA regulations require a number of these types of restrictions, although the economic efficiency of these requirements has not been examined.

4. PROMOTING PRIVATE DISEASE CONTROL EFFORTS

The bioeconomic decision framework can be used to identify desirable actions on both public and private lands (where desirability is defined according to the agencies’ preferences over those of various stakeholder groups). Agencies can implement many actions on public lands directly, such as supplemental feeding for elk. However, policy mechanisms are generally required to promote an agency’s preferred disease management strategies when private individuals are involved. This includes hunters on public and private lands and ranchers on private lands and public grazing areas—at least when these individuals choose risk mitigation and adaptation strategies that are inconsistent with an agency’s preferred strategy.

The following policy design discussion is framed around two important simplifications to facilitate understanding. First, policy development is described as if a single coordinating agency were responsible. Agency coordination is a challenge and is further discussed in section 4.3. Second, policy development targets the objective of efficiency. As described earlier, agencies may have other objectives, and various policy choices may affect distributional or equity outcomes that agencies might value.

4.1 The Need for Policy

Policies to promote risk mitigation and adaptation, collectively referred to as self-protection, may be needed even if hunters and ranchers already have some incentives for these measures based on their perceived benefits. For instance, hunters may choose to avoid high-prevalence elk herds rather than to engage in efforts to reduce the densities of these herds. Similarly, while ranchers have strong incentives to consider the private costs and benefits of self-protection, they will typically underinvest (relative to efficient levels) in self-protection activities that generate positive benefits to others (Baumol and Oates, 1988; Hanley et al., 1997). The private costs may outweigh the private benefits of many risk-management activities (Roberts et al., 2012), although these actions may also benefit society. The result of this under-investment is greater risk and lower social economic welfare. Public policies can provide the required impetus for ranchers to adopt more socially efficient levels of risk management.

*Revisiting Brucellosis in the Greater Yellowstone Area***4.2 Policy Design Choices**

Two questions need to be addressed in designing policies that encourage private individuals to engage in a particular disease-control strategy (Hanley et al., 1997; Shortle et al., 1998): first, what intended actions or outcomes will serve as the basis or compliance measure for policy mechanisms; second, what specific mechanisms will be used (e.g., economic incentives or a regulatory mandate, and the levels of these mechanisms)?

First Design Choice: The Compliance Measure

A compliance measure is simply an indicator of when sufficient efforts have been applied to satisfy a regulation, or when incentive payments are altered in response to change in efforts. Compliance measures may be defined in terms of particular actions, such as herd vaccination rates, which may be set by mandate or incentivized by subsidizing each unit (e.g., percentage) of the herd that is vaccinated. Alternatively, compliance measures may be defined in terms of some measure of actual or expected performance or outcome resulting from risk-management actions. An example of an actual performance outcome is the number of infected animals that are traced back to a particular ranch; a performance-based policy in this situation might be a tax per infected animal that is traced back to the herd. An example of expected performance is a modeled estimate of the probability a rancher's herd becomes infected and then spreads infection to other producers, conditional on the ranchers' risk-management actions; a performance-based subsidy might reward producers for reducing this modeled probability. In the present context, performance-based approaches are likely to be relevant only for ranchers, as it is difficult to imagine a performance-based approach that may be usefully applied to hunters. Risk models would have to be developed to calculate how various practices can reduce transmission probabilities, and then be made available to individual ranchers so that they can determine the risk impacts of their choices. The need to develop quantitative risk models does not need to be viewed as a drawback, because such models are already needed as a basis for any sound risk-management strategy. There is precedent for using risk modeling to implement performance-based approaches for other environmental problems where actual impacts are difficult to measure, including modeled estimates of nonpoint source nutrient pollution from agricultural fields (EPA, 2014) and the modeled probability that a ship introduces invasive species via its ballast water discharge (Karaminas et al., 2000).

In theory, policies based on actions or performance can work for ranchers; but, in practice, there are trade-offs associated with implementation. A policy instrument based on a single observable action would be the easiest to implement and could provide the clearest incentives because it is directly tied to a specific choice. However, many choices might have to be regulated or incentivized to produce the desired effect, and it may be difficult to ensure that each choice is properly regulated or incentivized, especially if there are considerable uncertainties over the parameters used to determine regulation or incentive levels. Errors in setting policy variables will result in individuals over- or underinvesting in the various risk-management actions, with these errors potentially becoming compounded when separate policy variables are applied to many choices.

Basing policies on expected performance does not reduce monitoring requirements (as it remains necessary to monitor the relevant choices that are provided as input into the predictive risk model), but it does reduce the number of policy variables, potentially reducing administrative costs and compounding errors. This approach is also advantageous because it gives private individuals the flexibility to decide how best to carry out risk-management activities. That is, a performance-based approach encourages individuals to improve their performance in the most efficient way possible by using their private knowledge of the costs for making decisions. The drawback of this approach is that individuals may have difficulty using the risk model to properly evaluate the impacts of their decisions.

*Economic Issues in Managing Brucellosis**Second Design Choice: Specific Policy Mechanisms*

The second design choice is determining the mechanisms for inducing behavioral changes. Regulations (such as standards that limit risky behaviors) and economic incentives (such as taxes on risk-increasing behaviors and subsidies on risk-reducing behaviors) are the primary options. Regulatory standards simply mandate particular behaviors or outcomes consistent with the agency's preferred strategy. In contrast, individuals facing incentives retain the flexibility to make their own decisions, although the incentives influence these decisions. Specifically, efficient tax or subsidy rates tied to an activity affecting disease risks would be set equal to the expected external economic impacts of the activity in the efficient outcome. These incentive rates then act as prices that cause individuals to consider the expected external social costs or benefits associated with their choices (Baumol and Oates, 1988). Education programs can play valuable supportive roles but improved knowledge about external benefits is generally inadequate to induce sufficient adoption of costly actions (Ribaudo and Horan, 1999; Horan et al., 2001; Shortle et al., 2012).

Grazing fees represent an example of incentives akin to a tax. Federal grazing fees are currently applied uniformly across the landscape without regard to brucellosis risks (Rimbey and Torell, 2011). By charging larger fees to access higher-risk grazing allotments, this would discourage and reduce access to higher-risk areas while not eliminating this opportunity for ranchers who believe it would be profitable. There is precedent to make grazing allotments dependent on disease risk, as the Bureau of Land Management (BLM) has recently made policy changes designed to separate bighorn and domestic sheep (BLM, 2016). Similar risk prevention policies on USFS- and BLM-administered grazing lands could be effective by encouraging the separation of cattle from elk during the period from late April through late June when most brucellosis-related abortions in elk occur.

Subsidies are often used to positively encourage landowners to change production or land uses on certain sites. For instance, subsidies could be used to encourage landowners to haze elk off their properties, to give hunters more access to private lands, or to implement their own wildlife population controls on private lands. This issue is particularly important given the growth in privately owned land in the GYA where elk may seek refuge from hunting (Schumaker et al., 2012). Economic studies are needed to explore what incentives would be required for landowners to participate in such disease control programs. Certain high-risk, low-profit producers could also be subsidized to cover the costs of permanently switching to alternative livestock or land use activities that do not involve the risk of brucellosis. Another option would be to buy out these producers, but that could be less beneficial to society than encouraging the land to be placed in an alternative, productive use.

Regulatory standards applied to an activity make the most sense when it is in society's best interest to prohibit flexibility on the effort level applied to that activity (in contrast to pricing mechanisms, which allow flexibility). A situation involving such an outcome is when the expected social benefits of a desirable change in effort (e.g., applying less effort to a risk-increasing activity, or applying more effort to a risk-reducing activity) always exceed the expected social costs of this change (Shortle and Abler, 1997).¹⁷ Examples involving risk-reducing efforts might include mandating efforts to prohibit contact among risky animals, such as regulations for quarantining animals and for always hazing elk away from cattle herds. An example involving a risk-increasing effort is to prohibit grazing in high-risk areas at high-risk times. In the case of grazing, this would require only simple modifications to the regulatory approach of a fixed entry

¹⁷Such an outcome, which is referred to as a corner solution, involves a wedge between expected marginal social benefits and expected marginal social costs. This wedge means that even a small change in effort can be highly costly. Therefore, if prices were to be applied in this setting, it might be in society's best interest to set them large enough that there would be little chance of producers deviating from the desired outcome. Note that the examples provided in the text involve cases where producers can vary effort levels. There might also be somewhat extreme cases where an activity is discretely defined, such that one either adopts a technology or does not (i.e., a particular producer cannot choose a degree of adoption). Regulations, possibly in conjunction with a cost-sharing component, might also be preferred in such situations to ensure that the correct technology is chosen.

Revisiting Brucellosis in the Greater Yellowstone Area

date for federal grazing that currently makes no consideration of brucellosis risks (Rimbey and Torell, 2011). Delaying access for grazing until after the elk birthing period would reduce risk.

Hunting permits represent a standard once the permits are distributed, although permit fees are essentially an incentive-based pricing mechanism (a tax) that allocates permits according to individuals' values for them. Optimally, permits (if distributed freely) or their prices would be defined spatially and temporally to better manage spatial and temporal risks. Permit levels might be increased, or permit prices decreased, in high-risk areas to encourage reductions in wildlife density. In cases where free distribution of permits in high-risk areas might generate insufficient hunting pressure, hunters would have to be paid to hunt or else resource managers would have to implement population controls directly.

Damage Compensation

To help ranchers endure disease risks, compensation for disease risks and income enhancement mechanisms are often advocated (e.g., WBCT, 2005). These approaches deserve special mention because they generally do not promote disease risk management and can instead generate perverse risk-management incentives. For instance, USDA's livestock indemnification program pays ranchers the fair market value of infected animals (Hoag et al., 2006; USDA-APHIS, 2016). This program may not fully compensate ranchers for all costs (e.g., business interruption, feeding and care costs for animals, and loss of markets), but it does significantly reduce a producer's losses. Fewer losses, combined with the fact that producers may not have to take special preventive actions to qualify for these payments, means that indemnities can reduce the expected costs of becoming infected. Consequently, ranchers have fewer incentives to protect their herds from infection (Hennessy et al., 2005; Muhammad and Jones, 2008; Gramig and Horan, 2011), potentially resulting in many producers operating in a risky environment (Baumol and Oates, 1988). Both of these features increase the overall disease risks to society and reduce expected social welfare.

Indemnity programs can be modified to address this problem. For instance, indemnities could be made contingent either on adopting certain observable biosecurity practices (Reeling and Horan, 2015) or on evidence of biosecurity measures being adopted (Gramig and Horan, 2011). An example of this concept is USDA's recent adjustments to highly pathogenic avian influenza indemnity payments to poultry producers (USDA-APHIS, 2016). Such approaches force agents to bear some risk of losses who otherwise would insufficiently invest in biosecurity, which ultimately incentivizes them to invest in mitigation. The conditions for indemnification can also be developed so that their biosecurity investments protect others in case their herd does become infected (Reeling and Horan, 2015).

Insurance programs to cover non-indemnified losses caused by disease are theoretically possible, but currently they do not exist (Grannis et al., 2004). Examples of related insurance programs include USDA's Livestock Risk Protection program (USDA, 2014) and USDA's recently developed Rainfall Index Pasture, Rangeland, Forage (PRF) pilot program (USDA, 2015). As with indemnities, insurance programs could reduce ranchers' risk-management incentives unless payments or premiums are tied to producer behavior. For instance, premiums might be subsidized for producers who provide evidence of investing in self-protection to reduce brucellosis risks. While an insurance program holds merit conceptually, there are a host of challenges and knowledge gaps. There will need to be sufficient interest by producers for such a program to be viable, since premiums are required to fund payouts. Also, livestock producers often implement fewer-than-expected risk management efforts despite extensive knowledge about the practices (Goodwin and Schroeder, 1994; Pennings and Garcia, 2001; Wolf and Widmar, 2014). This may limit the ability of program managers to modify insurance (and indemnity) programs to create risk-management incentives. There are situations where insurance works well and when it does not (Goodwin and Smith, 2013; Reeling and Horan, 2015), and whether these mechanisms might work well in the GYA is an empirical question that has yet to be addressed.

*Economic Issues in Managing Brucellosis**Equity Considerations*

Multiple mechanisms (taxes, subsidies, or regulations) may be capable of encouraging any particular risk-management action, but the mechanisms differ in terms of their equity impacts—that is, how the economic costs and benefits are distributed. For instance, subsidies involve private individuals being compensated by taxpayers for reducing social risks. Standards and taxes require private individuals to pay the costs of risk reduction activities (unless financial assistance is offered, in which case taxpayers share the burden). Additionally, taxes require the risk-generating agents to pay more and are politically controversial. However, taxes generate funds that could be used to offset the costs of other government activities, either now or in the future, to benefit current or future taxpayers. For instance, tax receipts could be used to fund risk-management activities by various agencies, or they could be used to fund subsidy programs to further reduce risk. Tax receipts could also be used to reallocate welfare within the GYA in a manner that is not tied to risk management—that is, as a lump sum payment not based on disease-related costs (and therefore not a compensation scheme).

Multiple policy mechanisms could lead to the same efficient outcome while distributing economic costs and benefits differently among stakeholders. This means that addressing equity concerns does not necessarily have to come at the expense of economic efficiency. Initial attempts to address equity concerns may therefore involve selecting the right combination of instruments. Further attempts to fine-tune the distribution of economic outcomes among stakeholders might be pursued using lump sum transfer payments that do not influence behaviors (e.g., redistributing a portion of grazing fees or hunting permit fees to all ranchers, regardless of risk-management decisions or infection outcomes). Once these two options have been exhausted, any further attempts to address equity concerns will have efficiency reducing consequences.

4.3 Agency Coordination

Many agencies are involved in managing brucellosis in the GYA, with each agency having its own mission and objectives along with its own stakeholder groups (e.g., NER and USFWS, 2014; IBMP, 2015). Even if all agencies agreed that efficient disease control is a desirable objective, agencies may be unable to coordinate their efforts because each may have other objectives and interests that supersede the level of effort and commitment needed to efficiently and effectively address brucellosis. A lack of coordination can result in limited efforts to manage brucellosis risks as well as limited collection and sharing of information that can improve opportunities for adaptive management.

One reason for coordination failure is that the agencies and associated stakeholder groups who gain most from disease control (e.g., USDA and ranchers) may not be the ones incurring the most costs (e.g., park and wildlife managers, hunters, conservationists, and park visitors). While it may be possible to negotiate a limited degree of coordination in this setting, agencies are unlikely to commit significant resources of their own or of their stakeholders when the benefits largely accrue to others. Promoting broader and more intensive coordination will generally require mechanisms that transfer wealth from agencies and stakeholders who gain from disease control to the agencies and stakeholders who bear the costs from disease control (Ostrom, 1990). Such an institutional arrangement would appear quite different from current collaborative approaches. For instance, the IBMP represents a collaborative strategy for bison negotiated by agencies with different incentives, with the execution and costs dependent on each agency rather than determined by a single organization considering the best interests of society as a whole. Devising mechanisms to share costs and benefits in ways that promote agency coordination is a major topic when developing international environmental agreements (especially those dealing with climate change [Barrett, 2003]) and when developing international defensive collaborations (such as NATO [Sandler, 1977]), and those lessons from other areas could be valuable for promoting coordination among agencies when equity appears to be a concern. In an adaptive management framework, opportunities for coordination are likely to be enhanced when wealth transfers are based on performance outcomes (e.g., reduced elk prevalence in an area) rather than on action-based outcomes (e.g., percent of elk vaccinated in the area) that may appear good in principle but

Revisiting Brucellosis in the Greater Yellowstone Area

may not produce the desired effect. It will be hard to sustain coordination if the coordinated strategy does not sufficiently improve the situation.

5. SUMMARY

Managing brucellosis in the GYA is unlikely to yield significant improvements unless the complex social dimensions of the problem are addressed. This will require evaluating trade-offs associated with many disparate interests, promoting cooperation among various regulatory agencies who oversee different facets of the GYA system, and using monetary and other resources wisely to reduce risks. This may involve altering the behaviors of individuals who interact with wildlife and livestock.

An economic valuation can be used to quantify the concerns of GYA stakeholders. A bioeconomic framework that treats the GYA as a coupled ecological-socioeconomic system can then be used to compute broadly defined, long-term costs and benefits associated with proposed brucellosis management strategies. This sort of simple cost-benefit analysis can help to evaluate proposed strategies. However, the power of the bioeconomic framework lies in its ability to be applied in a decision-making context to construct socially desirable strategies. In particular, a bioeconomic decision-making framework can help to identify economically efficient strategies that will generate the greatest net economic gains (benefits minus costs) to society as a whole, taking into account the many market and nonmarket values that our diverse society places on wildlife resources and cattle production both in the short run and the long run. Efficient strategies are likely to involve a variety of control measures that may be applied differentially over space and time to reflect variations in spatial-temporal risks and that target several types of risks to varying degrees: disease transmission among wildlife, cattle exposure to wildlife risks, and economic risks both in the GYA and beyond. Implementing disease control strategies requires coordination by a number of federal, state, and local agencies, which could be challenging because agencies and stakeholders who benefit from disease control are unlikely to be the ones bearing the costs. Mechanisms for sharing costs and benefits will be required for proper coordination and successful disease control.

REFERENCES

- Adamowicz, W., P. Boxall, M. Williams, and J. Louviere. 1998. Stated preference approaches for measuring passive use values: Choice experiments and contingent valuation. *American Journal of Agricultural Economics* 80(1):64-75.
- Allen, K. 2014. History lesson in packing plant closures. *Drovers*, August 12, 2014. Available online at <http://www.cattlenetwork.com/cattle-news/History-lesson-in-packing-plant-closures—270912481.html> (accessed January 11, 2017).
- Alston, J., and B.H. Hurd. 1990. Some neglected social costs of government spending in farm programs. *American Journal of Agricultural Economics* 72:149-156.
- Anderson, R.M., and R.M. May. 1979. Population biology of infectious diseases: Part I. *Nature* 280:361-367.
- Barbier, E.B. 2000. Valuing the environment as input: Review of applications to mangrove-fishery linkages. *Ecological Economics* 35(1):47-61.
- Barbier, E.B. 2011. *Capitalizing on Nature: Ecosystems as Natural Assets*. Cambridge, UK: Cambridge University Press.
- Barrett, S. 2003. *Environment and Statecraft: The Strategy of Environmental Treaty-Making*. New York: Oxford University Press.
- Baumol, W., and W. Oates. 1988. *The Theory of Environmental Policy*. Cambridge, UK: Cambridge University Press.
- Bicknell, K.B., J.E. Wilen, and R.E. Howitt. 1999. Public policy and private incentives for livestock disease control. *Australian Journal of Agricultural and Resource Economics* 43:501-521.
- BLM (Bureau of Land Management). 2016. Management of Domestic Sheep and Goats to Sustain Wild Sheep. Manual Transmittal Sheet MS 1730. March 2, 2016. Available online at http://www.blm.gov/style/medialib/blm/wo/Information_Resources_Management/policy/blm_manual.Par.40213.File.dat/MS%201730.pdf (accessed January 11, 2017).

Economic Issues in Managing Brucellosis

- Boroff, K., M. Kauffman, D. Peck, E. Maichak, B. Scurlock, and B. Schumaker. 2016. Risk assessment and management of brucellosis in the southern greater Yellowstone area (II): Cost-benefit analysis of reducing elk brucellosis prevalence. *Preventive Veterinary Medicine* 134:39-48.
- Boyle, K.J. 2003. Introduction to revealed preference methods. In *A Primer on Nonmarket Valuation*. P.A. Champ, K.J. Boyle, and T.C. Brown, eds. Dordrecht, The Netherlands: Kluwer.
- Chambers, R.G. 1988. *Applied Production Economics: A Dual Approach*. Cambridge: Cambridge University Press.
- Clark, C.W. 2005. *Mathematical Bioeconomics Optimal Management of Renewable Resources*, 2nd ed. Hoboken, NJ: Wiley.
- Costello, C., S.D. Gaines, and J. Lynham. 2008. Can catch shares prevent fisheries collapse? *Science* 321(5896):1678-1681.
- DEFRA (Department for Environment Food & Rural Affairs). 2014. The Strategy for Achieving Officially Bovine Tuberculosis Free Status for England. Available online at https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/300447/pb14088-bovine-tb-strategy-140328.pdf (accessed January 11, 2017).
- Duffield, J., C. Neher, and D. Patterson. 2006. *Wolves and People in Yellowstone: Impacts on the Regional Economy*. Bozeman, MT: Yellowstone Park Foundation.
- ECCFMD (European Commission for the Control of Foot-and-Mouth Disease). 2011. The Progressive Control Pathway for FMD Control (PCP-FMD): Principles, Stage Descriptions and Standards. Available online at http://www.oie.int/eng/A_FMD2012/docs/Background_papers_PCP_FMD.pdf (accessed January 11, 2017).
- EPA (U.S. Environmental Protection Agency). 2014. Accounting for Uncertainty in Offset and Trading Programs. EPA Technical Memorandum, February 12, 2014. Available online at https://www.epa.gov/sites/production/files/2015-07/documents/final_uncertainty_tm_2-12-14.pdf (accessed January 11, 2017).
- Fenichel, E.P., and R.D. Horan. 2007a. Gender-based harvesting in wildlife disease management. *American Journal of Agricultural Economics* 89:904-920.
- Fenichel, E.P., and R.D. Horan. 2007b. Jointly-determined ecological thresholds and economic trade-offs in wildlife disease management. *Natural Resource Modeling* 20:511-547.
- Fenichel, E.P., R.D. Horan, and G. Hickling. 2010. Management of infectious wildlife diseases: Bridging conventional and bioeconomic approaches. *Ecological Applications* 20:903-914.
- Fenichel, E.P., C. Castillo-Chavez, M.G. Ceddia, G. Chowell-Puente, P.A. Gonzalez-Parra, G.J. Hickling, G. Holloway, R.D. Horan, B. Morrin, C. Perrings, M. Springborn, L. Velazquez, and C. Villalobos. 2011. Adaptive human behavior in epidemiological models. *Proceedings of the National Academy of Sciences of the United States of America* 108:6306-6311.
- Fenichel, E.P., J.K. Abbott, J. Bayham, W. Boone, E.M.K. Haacker, and L. Pfeiffer. 2016. Measuring the value of groundwater and other forms of natural capital. *Proceedings of the National Academy of Sciences of the United States of America* 113(9):2382-2387.
- Finnoff, D., J.F. Shogren, B. Leung, and D. Lodge. 2005. The importance of bioeconomic feedback in invasive species management. *Ecological Economics* 52(3):367-381.
- Freeman, A.M., III. 1993. *The measurement of environmental and resource values: Theory and method*. Washington, DC: Resources for the Future.
- Freeman, A.M., III. 2003. Economic valuation: What and Why? In *A Primer on Nonmarket Valuation*. P.A. Champ, K.J. Boyle, and T.C. Brown, eds. Dordrecht, The Netherlands: Kluwer.
- Gardner, B.L. 1987. *The Economics of Agricultural Policies*. New York: MacMillan.
- Goodwin, B.K., and T.C. Schroeder. 1994. Human capital, producer education programs, and the adoption of forward-pricing methods. *American Journal of Agricultural Economics* 76(4):936-947.
- Goodwin, B.K., and V.H. Smith. 2013. What harm is done by subsidizing crop insurance? *American Journal of Agricultural Economics* 95:489-497.
- Gordon, H.S. 1954. The economic theory of a common-property resource: The fishery. *Journal of Political Economy* 62:124-142.
- Grafton, R.Q., and T. Kompas. 2005. Uncertainty and the active adaptive management of marine reserves. *Marine Policy* 29(5):471-479.
- Gramig, B.M., and R.D. Horan. 2011. Jointly determined livestock disease dynamics and decentralised economic behavior. *Agriculture and Resources Economics* 55(3):393-410.
- Grannis, J.L., J.W. Green, and M.L. Bruch. 2004. Animal health: The potential role for livestock disease insurance. *Western Economics Forum*, April 2004. Available online at <http://ageconsearch.umn.edu/bitstream/27972/1/03010001.pdf> (accessed January 11, 2017).
- Greene, W.H. 2017. *Econometric Analysis*. New York: Pearson.

Revisiting Brucellosis in the Greater Yellowstone Area

- Hanley, N., J.F. Shogren, and B. White. 1997. *Environmental Economics in Theory and Practice*. New York: Oxford University Press.
- Heesterbeek, J.A.P., and M.G. Roberts. 1995. Mathematical models for microparasites of wildlife. Pp. 90-122 in *Ecology of Infectious Diseases in Natural Populations*. B.T. Grenfell and A.P. Dobson, eds. New York: Cambridge University Press.
- Hennessy, D.A. 2007a. Behavioral incentives, equilibrium endemic disease, and health management policy for famed animals. *American Journal of Agricultural Economics* 89:698-711.
- Hennessy, D.A. 2007b. Biosecurity and spread of an infectious animal disease. *American Journal of Agricultural Economics* 89:1226-1231.
- Hennessy, D.A., J. Roosen, and H.H. Jensen. 2005. Infectious disease, productivity, and scale in open and closed animal production systems. *American Journal of Agricultural Economics* 87:900-917.
- Hoag, D.L., D.D. Thilmany, and S.R. Koontz. 2006. Economics of livestock disease insurance—Principles, issues and worldwide cases. Pp. 1-18 in *The Economics of Livestock Disease Insurance: Concepts, Issues and International Case Studies*. S.R. Koontz, D.L. Hoag, D.D. Thilmany, J.W. Green, and J.L. Grannis, eds. Wallingford, UK: CABI.
- Hobbs, N.T., C. Geremia, J. Treanor, R. Wallen, P.J. White, M.B. Hooten, and J.C. Rhyan. 2015. State-space modeling to support management of brucellosis in the Yellowstone bison population. *Ecological Monographs* 85(4):525-556.
- Holmes, T.P., and W.L. Adamowicz. 2003. Attribute-based methods. Pp. 161-219 in *A Primer on Nonmarket Valuation*. P.A. Champ, K.J. Boyle, and T.C. Brown, eds. Dordrecht, The Netherlands: Kluwer.
- Horan, R.D., and E.P. Fenichel. 2007. Economics and ecology of managing emerging infectious animal diseases. *American Journal of Agricultural Economics* 89:1232-1238.
- Horan, R.D., and R.T. Melstrom. 2011. No sympathy for the devil. *Journal of Environmental Economics and Management* 62(3):367-385.
- Horan, R.D., and C.A. Wolf. 2005. The economics of managing infectious wildlife disease. *American Journal of Agricultural Economics* 87:537-551.
- Horan, R.D., M.O. Ribaud, and D.G. Abler. 2001. Voluntary and indirect approaches for reducing externalities and satisfying multiple objectives. Pp. 67-84 in *Environmental Policies for Agricultural Pollution Control*. J.S. Shortle, and D.G. Abler, eds. Oxfordshire, UK: CABI.
- Horan, R.D., C.A. Wolf, E.P. Fenichel, and K.H. Mathews, Jr. 2008. Joint management of wildlife and livestock disease. *Environmental and Resource Economics* 41:47-70.
- Horan, R.D., E.P. Fenichel, C.A. Wolf, and B.M. Gramig. 2010. Managing infectious animal disease systems. *Annual Review of Resource Economics* 2:101-124.
- Horan, R.D., E.P. Fenichel, D. Finnoff, and C.A. Wolf. 2015. Managing dynamic epidemiological risks through trade. *Journal of Economic Dynamics and Control* 53:192-207.
- IBMP (Interagency Bison Management Plan). 2015. Annual Report of the Interagency Bison Management Plan: November 1, 2014, through October 31, 2015. December 2015. Available online at http://www.ibmp.info/Library/AnnualReports/2015_IBMP_AnnualReport_final.pdf (accessed January 11, 2017).
- Just, R.E., D.L. Hueth, and A. Schmitz. 1982. *Applied Welfare Economics and Public Policy*. Englewood Cliffs, NJ: Prentice Hall.
- Just, R.E., D.L. Hueth, and A. Schmitz. 2005. *The welfare economics of public policy: A practical approach to project and policy evaluation*. Cheltenham, UK: Edward Elgar Publishing.
- Karaminas, L., H.H. Ocakli, K.C. Mazdon, and P.C. Westlake. 2000. *Ballast Water Management*. LR Technical Association Paper no. 1, Session 2000-2001. London, UK: Lloyd's Register of Shipping.
- Kauffman, M.E., B.S. Rashford, and D.E. Peck. 2012. Unintended consequences of bovine brucellosis management on demand for elk hunting in northwestern Wyoming. *Human-Wildlife Interactions* 6:12-29.
- Leung, B., D.M. Lodge, D. Finnoff, J.F. Shogren, M.A. Lewis, and G. Lamberti. 2002. An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society of London B* 269:2407-2413.
- Loomis, J., and L. Caughlan. 2004a. Economic analysis of alternative bison and elk management practices on the National Elk Refuge and Grand Teton National Park: A Comparison of Visitor and Household Responses. U.S. Geological Survey, Open-File Report 2004-1305.
- Loomis, J., and L. Caughlan. 2004b. Linking Intended visitation to regional economic impact models of bison and elk management. *Human Dimensions of Wildlife* 9:17-33.
- MacLachlan, M.J., M.R. Springborn, and P.L. Fackler. 2017. Learning about a moving target in resource management: Optimal Bayesian disease control. *American Journal of Agricultural Economics* 99(1):140-162.

Economic Issues in Managing Brucellosis

- Mahul, O., and A. Gohin. 1999. Irreversible decision making in contagious animal disease control under uncertainty: An illustration using FMD in Brittany. *European Review of Agriculture Economics* 26:39-58.
- Maichak, E.J., B.M. Scurlock, P.C. Cross, J.D. Rogerson, W.H. Edwards, B. Wise, S.G. Smith, and T.J. Kreeger. 2017. Assessment of a strain 19 brucellosis vaccination program in elk. *Wildlife Society Bulletin*. DOI: 10.1002/wsb.734.
- Mazzanti, M. 2003. Valuing cultural heritage in a multi-attribute framework microeconomic perspectives and policy implications. *The Journal of Socio-Economics* 32:549-569.
- Meatingplace. 2014. Dry Age Beef. Available online at <http://dryagebeef.meatingplace.com> (accessed January 11, 2017).
- McCollum, D.W. 2003. Nonmarket valuation in action. Pp. 483-535 in *A Primer on Nonmarket Valuation*. P.A. Champ, K.J. Boyle, and T.C. Brown, eds. Dordrecht, The Netherlands: Kluwer.
- McInerney, J.P., K.S. Howe, and J.A. Schepers. 1992. A framework for the economic analysis of disease in farm livestock. *Preventive Veterinary Medicine* 13:137-154.
- MDARD (Michigan Department of Agriculture and Rural Development). 2011. Bovine Tuberculosis: Bovine TB Split State Status and Zoning Rules. Available online at https://www.michigan.gov/documents/emergingdiseases/bovine_TB_SSS_Zoning_Final_as_of_9-26-11_364559_7.pdf (accessed January 11, 2017).
- Mueller, D.C. 1989. *Public Choice II*. Cambridge, MA: Cambridge University Press.
- Muhammad, A., and K. Jones. 2008. The impact of federal indemnification on livestock biosecurity. *Economics Bulletin* 17(10):1-9.
- NER/USFWS (National Elk Refuge and U.S. Fish & Wildlife Service). 2014. Draft Comprehensive Conservation Plan and Environmental Assessment: National Elk Refuge. Jackson, Wyoming. August 2014. Available online at https://www.fws.gov/mountain-prairie/planning/ccp/wy/ner/documents/ner_draftccp_all.pdf (accessed January 11, 2017).
- NRC (National Research Council). 2004. *Valuing Ecosystem Services: Toward Better Environmental Decision-Making*. Washington, DC: The National Academies Press.
- Ostrom, E. 1990. *Governing the Commons*. Cambridge, UK: Cambridge University Press.
- Parsons, G.R. 2003. The travel cost model. Pp. 269-329 in *A Primer on Nonmarket Valuation*. P.A. Champ, K.J. Boyle, and T.C. Brown, eds. Dordrecht, The Netherlands: Kluwer.
- Pennings, J.M.E., and P. Garcia. 2001. Measuring producers' risk preferences: A global risk-attitude construct. *American Journal of Agricultural Economics* 83:993-1009.
- Perrings, C. 2005. Mitigation and adaptation strategies for the control of biological invasions. *Ecological Economics* 52:315-325.
- Rausser, G. 1982. Political economic markets, PERTs and PESTs in food and agriculture. *American Journal of Agricultural Economics* 64(5):821-833.
- Rausser, G.C., and W.E. Foster. 1991. The evolution and coordination of U.S. commodity and resources policy. Pp. 17-45 in *Commodity and Resources Policy in Agricultural Systems*. R.E. Just and N. Bockstael, eds. Berlin, Germany: Springer.
- Ready, R.C., and S. Navrud. 2002. Methods for valuing cultural heritage. Chapter 2 in *Valuing cultural heritage: Applying environmental valuation techniques to historical building monuments and artifacts*. S. Navrud and R.C. Ready, eds. Cheltenham, UK: Edward Elgar Publishing.
- Reeling, C., and R.D. Horan. 2015. Self-protection, strategic interactions, and the relative endogeneity of disease risks. *American Journal of Agricultural Economics* 97:452-468.
- Ribaudo, M.O., and R.D. Horan. 1999. The role of education in nonpoint source pollution control policy. *Review of Agricultural Economics* 21:331-343.
- Rimbey, N., and L.A. Torell. 2011. Grazing Costs: What's the Current Situation? *Agricultural Economics Extension Series No 2011-02*, March 22, 2011. Moscow, ID: University of Idaho. Available online at <https://www.uidaho.edu/~media/UIIdaho-Responsive/Files/cals/Programs/ID-Agbiz/Publications/Grazing-Cost-2011.ashx> (accessed May 26, 2017).
- Roberts, M.B., and J.A.P. Heesterbeek. 2003. A new method for estimating the effort required to control an infectious disease. *Proceedings of the Royal Society B Biological Sciences* 270(1522):1359-1364.
- Roberts, T.W., D.E. Peck, and J.P. Ritten. 2012. Cattle producers' economic incentives for preventing bovine brucellosis under uncertainty. *Preventive Veterinary Medicine* 107(3-4):187-203.
- Ruff, S.P., D.E. Peck, C.T. Bastian, and W.E. Cook. 2014. Enterprise budget for a cow-calf-yearling operation, North-western Wyoming. Publication MP-120.1. University of Wyoming. Available online at <http://www.wyoextension.org/agpubs/pubs/MP-126.1.pdf> (accessed May 26, 2017).

Revisiting Brucellosis in the Greater Yellowstone Area

- Ruff, S.P., D.E. Peck, C.T. Bastian, and W.E. Cook. 2016. Economics of transitioning from a cow-calf-yearling operation to a stocker operation. 2016 *Journal of the American Society of Farm Managers and Rural Appraisers* 2016:55-76.
- Sandler, T. 1977. Impurity of defense: An application to the economics of alliances. *Kyklos* 30:443-460.
- Schumaker, B.A., D.E. Peck, and M.E. Kauffman. 2012. Brucellosis in the Greater Yellowstone Area: Disease management at the wildlife-livestock interface. *Wildlife Interactions* 6:48-63.
- Shortle, J.S., and D.G. Abler. 1997. Nonpoint pollution. Pp. 114-155 in *International Yearbook of Environmental and Natural Resource Economics*. H. Folmer and T. Teitenberg, eds. Cheltenham, UK: Edward Elgar Publishing.
- Shortle, J.S., R.D. Horan, and D.G. Abler. 1998. Research issues in nonpoint pollution control. *Environmental and Resource Economics* 11:571-585.
- Shortle, J.S., M.O. Ribaud, R.D. Horan, and D. Blandford. 2012. Reforming agricultural nonpoint pollution policy in an increasingly budget-constrained environment. *Environmental Science & Technology* 46(3):1316-1325.
- Springborn, M., and J.N. Sanchirico. 2013. A density projection approach for non-trivial information dynamics: Adaptive management of stochastic natural resources. *Journal of Environmental Economics and Management* 66(3):609-624.
- Stiglitz, J. E. 1987. Pareto Efficient and Optimal Taxation and the New Welfare Economics, in *Handbook of Public Economics*. A. J. Auerbach and M. Feldstein, eds. New York: North-Holland.
- Tonsor, G.T., T.C. Schroeder, and J.L. Lusk. 2013. Consumer indifference to alternative meat origin labels. *Journal of Agricultural Economics* 64(3):676-692.
- USDA (U.S. Department of Agriculture). 2014. Livestock Risk Protection Feeder Cattle. Risk Management Agency Fact Sheet May 2014. Available online at <http://www.rma.usda.gov/pubs/rme/lrp-feeder-cattle.pdf> (accessed January 11, 2017).
- USDA. 2015. USDA Expands Forage Crop Insurance Option Nationwide for Livestock Producers. News Release No. RMA-15-138. August 31, 2015. Available online at <http://www.rma.usda.gov/news/2015/08/forage-nationwide.pdf> (accessed January 11, 2017).
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2012. National Bovine Brucellosis Surveillance Plan. October 2012. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/nat_bruc_surv_plan.pdf (accessed January 11, 2017).
- USDA-APHIS. 2016. Conditions for Payment of Highly Pathogenic Avian Influenza Indemnity Claims, February 6, 2016. Available online at <http://www.regulations.gov/#!documentDetail;D=APHIS-2015-0061-0001> (accessed May 25, 2017).
- USDOI/USDA (U.S. Department of the Interior and U.S. Department of Agriculture). 2000. Record of Decision for Final Environmental Impact Statement and Bison Management Plan for the State of Montana and Yellowstone National Park, December 20, 2000. U.S. Department of the Interior, National Park Service, and U.S. Department of Agriculture, U.S. Forest Service, Animal and Plant Health Inspection Service. Available online at <https://www.nps.gov/yell/learn/management/upload/yellbisonrod.pdf> (accessed January 4, 2017).
- USFWS/NPS (U.S. Fish & Wildlife Service and National Park Service). 2007. Bison and Elk Management Plan: National Elk Refuge & Grand Teton National Park. April 2007. Available online at <http://www.fws.gov/bisonandelkplan> (accessed January 5, 2017).
- Varian, H.R. 1993. *Microeconomic Analysis*, 3rd ed. New York: W.W. Norton & Co.
- Walters, C.J. 1986. *Adaptive Management of Renewable Resources*. New York: Macmillan.
- WBCT (Wyoming Brucellosis Coordination Team). 2005. Report & Recommendations. January 11, 2005. Available online at http://www.wyomingbrucellosis.com/_pdfs/brucellosisCoordReport.pdf (accessed January 4, 2017).
- Wolf, C.A., and N.J.O. Widmar. 2014. Adoption of milk and feed forward pricing methods by dairy farmers. *Journal of Agricultural and Applied Economics* 46:527-541.

Remaining Gaps for Understanding and Controlling Brucellosis

1. INTRODUCTION

Critical knowledge gaps remain that limit understanding, detecting, and preventing the transmission of *Brucella abortus* in the Greater Yellowstone Area (GYA). Research to fill those knowledge gaps is needed in disease ecology, economics, immunology, vaccines and their delivery mechanisms, animal and pathogen genomics, and diagnostics. Research funding and expertise will need to be expanded to include other disciplines (such as disease ecology and epidemiology) for addressing gaps in the immediate term while also examining immunology, vaccines, and genomics for applications that would address gaps over the longer term. In this chapter, the committee provides an overview of some of the remaining gaps and research areas to pursue.

2. DISEASE ECOLOGY

Due to agency and jurisdictional boundaries and different mandates, there have been no major analyses of the epidemic across the tristate region of Idaho, Montana, and Wyoming. A major analysis is required to better understand the factors that are potentially driving the spatial spread of the disease in some regions but not others. A tristate approach may aid in understanding the roles of land use and predation on brucellosis in elk as well as the potential for transmission from elk to cattle and bison (both domestic and wild). Understanding the past and modeling the future spatial dynamics of brucellosis in elk will also require additional assessments of how elk populations are connected to one another.

Future land use and changing human demographics in the GYA are understudied and are likely to be important components of this system. From 1970-1999, the GYA has experienced a 58% increase in population and a 350% increase in exurban housing (Gude et al., 2006). These developments are disproportionately located on highly productive soils and lands close to water, which are also important wildlife winter ranges throughout the GYA. Many of these newer homeowners are less likely than the previous owners to allow public hunting, and this has created areas where elk are difficult for hunters to access and are “out of administrative control” (Haggerty and Travis, 2006). Although elk populations have declined within Yellowstone National Park (YNP), most of the surrounding elk populations have been stable or increasing such that some are five to nine times larger than they were in the 1970s and 1980s. Hunting license fees and the remittance of half of federal taxes on arms and ammunition (per the Pittman-Robertson Act of 1937) are the primary source of support for most state game and fish agencies, although the number of hunters has decreased in many regions (Winkler and Warnke, 2013; Schorr et al., 2014). These factors have potentially created a dynamic that may be detrimental to wildlife winter ranges across the GYA and also limited the funds and management tools available to state wildlife agencies. The relative proportion of ranchlands that turn over from livestock production to subdivisions or amenity owners that restrict hunting access is likely to be critical to the future ecological dynamics of wildlife winter ranges in the GYA and is an important aspect for future research.

There are benefits and drawbacks for expanding the existing boundaries of the designated surveillance areas (DSAs). Expanding the boundaries would expand the surveillance area and the increased scrutiny would decrease the likelihood that cattle may be infected outside the DSA and inadvertently moved to other

Revisiting Brucellosis in the Greater Yellowstone Area

regions and states, which could result in significant detection delays and expensive cleanup campaigns. Boundary expansion would thus be a potentially beneficial option for nationwide protection. However, DSA expansion would increase testing and management costs for state agencies and stigmatize some ranchers within the DSA, which are at a relatively low risk. Current boundaries are primarily based on judgment rather than quantitative optimization and are established independently by each state. To date, there has been no assessment of the risks of cattle being infected outside of DSAs. To determine the best way to draw DSA boundaries, a quantitative risk assessment could be used that combines information on elk densities, seroprevalence, and cattle locations.

It is unknown how unfed elk populations can maintain brucellosis at seroprevalence levels that are similar to or exceed those of elk on the supplemental feedgrounds in Wyoming. Scavengers may play a role by removing infectious fetuses from the landscape, and scavenging rates appear to be faster on supplemental feedgrounds than elsewhere. To determine if scavenging is an important factor in reducing cattle risk of infection or elk-to-elk transmission, studies need to be conducted on the potential negative effects of coyote control efforts by the Wildlife Services division of the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS) as well as the lack of any hunting regulations on coyotes in any of the three GYA states.

Host-parasite systems are almost never isolated, and the amount of cross-species transmission that occurs between elk and bison is unknown. Recent estimates only provide the number of transition events for the currently available isolates rather than estimating actual transmission rates per unit time in different locations (Kamath et al., 2016). This level of resolution is difficult to achieve and is unavailable for any wildlife system. It is an important area for future research that could be addressed by combining disease dynamic models into the phylogenetic framework (Stadler et al., 2014). In addition, little work has been done on the potential effects of other pathogens on brucellosis dynamics (Hines et al., 2007; Ezenwa and Jolles, 2015).

Serological tests are one of the best ways available to monitor population-level trends of brucellosis in wildlife species. Sample collection kits have been given to hunters in Idaho, Montana, and Wyoming. Combined with research-related captures, information from those kits provide more complete data from a broad region. Older wildlife individuals are generally more likely to test positive on serological assays due to having a longer time span for potential exposures to occur and for detectable antibody levels to develop after exposure. Extreme shifts in elk age distributions could be responsible for an approximate doubling in the raw seroprevalence (Cross et al., 2007). Serological assays differ in sensitivity and specificity, and therefore seroprevalence data need to be standardized to account for potential age and assay effects prior to comparisons across regions and time spans. Epidemiologists have traditionally addressed this issue by statistically estimating the effects of age, sex, and other heterogeneities, and then standardized rates to a common population before representing spatial variation (Ahmad et al., 2001; Osnas et al., 2009). Standardization by age, sex, or assay has not yet occurred across the GYA dataset, and there are no strong predictors of why one ranch may be more likely to be infected than another in the same general area. Case-control studies as well as fine scale risk assessments evaluating elk space-use data may help to assess the efficacy of different biosecurity measures.

Finally, while one study has examined elk-cattle contact rates (zu Dohna et al., 2014), there have been no studies investigating elk-cattle contact rates in the GYA where such studies are most needed. For example, a study could examine the effects of salt licks on grazing allotments as a factor enhancing elk-cattle contact. The lack of studies may be due to current regulatory rules requiring cattle testing for any known elk-cattle contact. This regulatory stipulation may also reduce the likelihood of producers to come forward and participate in elk-cattle contact studies.

3. ECONOMICS

Much information required to calibrate and integrate economic and disease ecology models is unavailable. More information is needed on the effectiveness and costs of various actions for reducing transmission.

Remaining Gaps for Understanding and Controlling Brucellosis

One category of missing information is nonmarket values associated with GYA wildlife. This includes use values (e.g., park visitation, wildlife viewing inside and outside the park, and hunting), and nonuse values (e.g., conservation of wildlife stocks, and management actions perceived as undesirable, such as mass culls and culls within park boundaries). All these values need to be specified as functions of bison and elk. One of the most relevant studies in providing such information examined the economic value of various bison and elk management practices for the National Elk Refuge and Grand Teton National Park (Loomis and Caughlan, 2004). However, those values are tied to the particular (ad hoc) management scenarios being analyzed, which impact multiple wildlife populations and make it difficult to identify the various economic values associated with changes in individual wildlife populations. Another relevant study more directly examines hunter demand for elk permits as a function of elk and wolf populations, but only for northwest Wyoming (Kauffman et al., 2012).

Several other types of economic information involving private landowners are also required for a bioeconomic analysis. For instance, surveys are required to acquire information on social and private incentives for separating cattle from elk, both on private lands (e.g., hazing) as well as public lands (e.g., spatial-temporal grazing decisions). Roberts and colleagues (2012) surveyed ranchers to estimate the costs of implementing various risk-management practices on an average farm in the southern GYA; however, the effectiveness of these practices, along with the associated benefits to ranchers and society, remains uncertain. Ruff and colleagues (2016) analyzed the costs and risks at which producers would break even from adopting various practices, but their analysis does not indicate how much effort needs to be applied or the point at which producers would break even from adopting various practices. Moreover, these analyses do not address social incentives for investment in terms of the risk that infected cattle might pose to herds of other producers within and outside the DSA. Economic information is also required about alternative land uses that would pose less or no risk from brucellosis. Economic information is also needed on incentives that might discourage landowners from managing lands as elk habitat/refuge. Lastly, focused research is needed to determine the impact of altering available grazing dates or grazing fees on both cattle grazing and the risk of spreading brucellosis.

4. IMMUNOLOGY

Developing new vaccines, especially ones that are effective in elk and that are more effective for cattle and bison than the existing ones, will require an understanding of how host protective immune responses are elicited. Tools to evaluate immune responses will be needed, especially for elk and bison as few currently exist. Researchers would find these tools useful, but there is unlikely to be a commercial interest in developing them; thus, funding will need to be sponsored by alternative sources (e.g., government grants). Other tools, such as methods to redirect immune responses toward protective immunity, are needed to prevent or treat infectious diseases. However, they are less likely to be developed for treating *Brucella*-infected wildlife or domestic livestock in the near term but could be considered as part of the long-term research goals.

4.1 Tools to Measure Immune Responses

Defining the nature of a protective immune response to virulent field strains of *Brucella* spp. will be important for designing new vaccines for brucellosis that induce such responses, determining the correlates of protection for evaluating potential vaccines and designing innovative treatments for infected animals. The protective immune response for brucellosis involves a type of white blood cell known as a T lymphocyte (or T cell) that is able to produce a soluble product known as cytokine interferon-gamma (IFN- γ). The response may also involve T cells that are able to kill bacteria-infected host cells. These types of T cell responses, known as cellular or cell-mediated responses, are needed because *Brucella* spp. resides in host cells such as macrophages and trophoblasts (Anderson and Cheville, 1986). IFN- γ activates macrophages to increase their ability to prevent replication of the internalized bacteria (Jiang and Baldwin, 1993). This mechanism of resistance is more effective than antibodies (Pavlov et al., 1982; Araya et al., 1989; Araya

Revisiting Brucellosis in the Greater Yellowstone Area

and Winter, 1990; Oliveira and Splitter, 1995; Goenka et al., 2011). In contrast to T cells, antibodies contribute only moderately to protection in secondary responses (challenge) with *B. abortus*; alone, they are less effective or contribute minimally to protection against a primary infection as suggested from murine studies (Goenka et al., 2011; Vitry et al., 2012). The need for cellular immune responses is also why live vaccines are more effective at protection than killed vaccines (Montaraz and Winter, 1986; Avila-Calderon et al., 2013), because the latter tends to induce immune responses that suppress the protective IFN- γ response (Zhan et al., 1995). For example, killed whole cell vaccines for *Brucella* have been shown to be ineffective in cattle (Olsen et al., 2005). The commercial vaccine consisting of killed *B. abortus* rough strain 45/20 is less effective than the living attenuated *B. abortus* strain 19 (S19) vaccine in conferring protection in cattle (Sutherland et al., 1981; Woodward and Jasman, 1983), which is attributed to the inability of killed vaccines to adequately stimulate cell-mediated immunity needed for protection (Nicoletti and Winter, 1990).

Assessing the efficacy of new vaccine candidates in elk and bison will require key reagents such as monoclonal antibodies (mAbs) to measure the types of cells that respond to vaccination and their products, such as IFN- γ production by T lymphocytes, which are considered to be a correlate of protective immunity. Because bison and cattle are genetically closely related, many of the bovine-specific mAbs are cross-reactive for bison lymphocytes and have aided in defining bison cell populations (Nelson et al., 2010). However, compared to the mouse model, there are fewer tools to study the immune responses in cattle and even fewer or none for bison and elk. Hence, tools are needed to evaluate all aspects of the innate and adaptive immune responses to understand why elk fail to produce robust cellular immune responses compared to the *Brucella* vaccines and other bacterial vaccines that stimulate appropriate immune responses in cattle and bison. This may require the development of species-specific brucellosis vaccines. Developing reagents (e.g., mAbs) is a slow and expensive process, but other techniques (e.g., the use of cytokine mRNA) can provide insights into the host immune response in the absence of mAbs. Also, high-throughput sequencing can evaluate elk or bison mRNA transcripts in response to vaccine candidates or during an infection, which is further discussed later in this chapter. All these tools require research and development.

4.2 Immunotherapy Post-Exposure

The ability to treat cattle post-exposure to brucellosis would be a useful management tool. Use of single antibiotics is not successful, but a combination treatment can eliminate shedding from the milk in up to 71% of animals (Milward et al., 1984; Nicoletti et al., 1985, 1989). However, even when combined with adult vaccination with *B. abortus* S19, the infection was controlled but not eliminated (Jimenez de Bagues et al., 1991). While combinations of aureomycin plus streptomycin (Kuppuswamy, 1954) or tetracyclines plus streptomycin have produced satisfactory results (Giaffret and Sanches, 1974; Marin et al., 1989), it does not result in loss of the lesions characteristic of this disease (Marin et al., 1989). Thus, other approaches will need to be considered and developed for post-infection treatments.

Immunotherapy or therapeutic vaccines have been associated with the cancer-causing human papilloma virus, hepatitis B infections, and the human immunodeficiency virus (HIV) (Jacobson et al., 2016; Lin et al., 2016; Skeate et al., 2016). Therapeutic vaccines may stimulate immune responses to components of the infectious organism that are not normally recognized by the immune system (known as antigens) because their concentration is typically too low or sequestered in particular tissues. Alternatively, they may redirect a protective immune response. This can be done by providing antigens in the context of enhancing agents (known as adjuvants); this may include cytokines such as IL-12 to orchestrate IFN- γ -producing T cell responses (Jacobson et al., 2016; Pennock et al., 2016). Finally, these vaccines could be designed to reengage immune cells that have undergone immunological exhaustion or been prohibited from expressing their protective potential by regulatory cells and molecules. The latter has been applied in cancer immunotherapy, for example, by blocking the T cell inhibitory molecule CTLA-4 (Callahan et al., 2016). While appealing, it is unlikely that immunotherapeutic vaccines will be a near-term accomplishment, but they could be considered as part of a research program.

Remaining Gaps for Understanding and Controlling Brucellosis

5. VACCINES AND DELIVERY MECHANISMS

New vaccines and methods of delivery are needed to improve the efficacy of current and future brucellosis vaccines. *B. abortus* vaccines need to be engineered to not cause disease or abortion in wildlife while still retaining sufficient persistence to stimulate long-term protection. While live *Brucella* vaccines have been shown to be necessary to induce protective immune responses in cattle, there is evidence that this can be mimicked by taking genes that code for components of *Brucella* and placing them into another microbe, which acts as a vector for the *Brucella* genes and mimics a live vaccine, but which may be safer than live, attenuated whole *Brucella* organisms (Dorneles et al., 2014). Live vaccines can be rendered less virulent by removing genes as well (Chen and Elberg, 1969). Other types of vaccines, that also have a high safety quotient, include DNA and subunit vaccines that deliver a portion of the *Brucella* genome or physical components of *Brucella* rather than the whole organism. Delivering vaccines in bait to wildlife is appealing, and conventional live vaccines *B. abortus* strains RB51 and S19 are effective when given orally and are safe in wildlife. It is possible that alternative vaccines could also be delivered this way. Finally, designing new vaccines with particular components either deleted or new components added would help distinguish vaccinated animals from actual infected animals (known as DIVAs [Distinguish Infectious from Vaccinated Animals]).

5.1 Alternative Delivery Methods for Vaccines

To date, the methods used to vaccinate wildlife are similar to those adopted for cattle (i.e., subcutaneous [SC] or intramuscular [IM]). Given that the initial exposure to *Brucella* almost always occurs mucosally because animals sniff or lick *Brucella*-infected aborted fetuses and/or infected placental tissues, delivery of the vaccine via a mucosal surface could result in an immune response that would induce greater protection (Thorne and Morton, 1978; Samartino and Enright, 1993; Belyakov and Ahlers, 2009; Schumaker, 2013). For example, it has been shown that mucosal vaccination can produce a bias for IFN- γ -producing CD8+ T cells (Clapp et al., 2011, 2016). Oral vaccination studies in cattle and pigs have shown the benefits of such an approach (Nicoletti and Milward, 1983; Nicoletti, 1984; Elzer et al., 1998; Edmonds et al., 2001). Oral S19 vaccination proved to be equally as effective as SC vaccination in protecting pregnant heifers from *Brucella*-induced abortion (Nicoletti and Milward, 1983; Nicoletti, 1984). Administering RB51 vaccine orally protected against abortion and brucellae colonization infection, and it provided equivalent results as SC RB51 vaccination (Elzer et al., 1998). Also, wildlife showed no morbidity or mortality as a consequence of oral RB51 vaccination (Januszewski et al., 2001). Oral vaccines also have ease of administration since they are needle-free and do not require trained personnel. Oral vaccines are subject to enzymatic and proteolytic degradation in the gastrointestinal tract, which can compromise the vaccine's immunogenicity, but drug formulations are available to counter this effect (Sedgmen et al., 2004). Additional engineering design and testing will be needed to orally vaccinate elk, such as developing baits targeted for elk. A mucosal approach has merit both for live, attenuated *B. abortus* vaccines and for vectored or subunit vaccines.

To reduce the need to handle animals more than once, an emerging and effective alternative to prime-boost vaccination is the use of microparticles or nanoparticles for sustained vaccine release (Lin et al., 2015). Biodegradable polymers are designed with specific release rates to mimic booster immunizations and induce anamnestic immune responses. This approach was tested using brucellosis-free red deer (*Cervus elaphus elaphus*), which are closely related to elk. Seven months after vaccination, animals were challenged with *B. abortus* S19 by the conjunctival route, and 2 weeks later the red deer that were orally vaccinated with RB51 microencapsulated in alginate plus *Fasciola hepatica* vitelline protein B (VpB) were the only ones that showed significant reduction in splenic colonization (Arenas-Gamboa et al., 2009a). This also demonstrates that microencapsulated S19 is protective against wild type virulent *B. abortus* challenge in female red deer (Arenas-Gamboa et al., 2009b). The development of vectors for safely transmitting vaccines to target wildlife populations, especially through feed, has been shown to be possible for vaccines against rabies and could also be considered for brucellosis (WHO, 2017).

5.2 Alternative Vaccine Approaches

Cross-protective vaccines. Several different approaches could be employed in designing new vaccines for elk and bison. Live vaccines could include a different *Brucella* species that is cross-protective to *B. abortus*. While *Brucella* species vary in their LPS, they retain many of the immunogenic proteins that could cross-protect against *B. abortus* infections. Reduced incidence of abortion attributed to *B. abortus* and *B. melitensis* was observed in Kuwait following a S19 brucellosis vaccination program of cattle (al-Khalaf et al., 1992). Reduced incidence of *B. melitensis* infections in humans was also observed following vaccination with *B. abortus* S19 (Vershilova, 1961). When *B. neotomae* (the strain originally found in desert wood rats) was irradiated and used to vaccinate mice, it also conferred 100 to 1,000-fold level of protection against *B. abortus*, *B. melitensis*, and *B. suis* (Moustafa et al., 2011). This study showed that irradiated organisms (which are living but cannot replicate) may be an alternative to strictly live vaccines.

Subunit and vectored vaccines. To generate a novel vaccine for cattle, influenza virus was used as a vector to express two immunodominant *Brucella* proteins: L7/L12 and omp16 (Tabynov et al., 2014). The immune responses to these proteins have been shown to reduce brucellae colonization in mice. Heifers vaccinated subcutaneously and conjunctivally showed 90% and 80% protection against abortion, respectively, compared to only 30% in the control heifers. To understand the duration of protective immunity to *Brucella* as measured by tissue brucellae colonization infection and abortion, a subsequent study used a reduced dose which showed a similar level of protection against abortion (Tabynov et al., 2016). The results from these studies for vectored vaccines suggest a subunit vaccine approach may be feasible for protecting large animals against *Brucella*-induced abortions. Identifying suitable vaccine candidates has been extensively pursued and tested in mice (Yang et al., 2013). It remains to be determined whether these vaccine candidates can successfully protect livestock and wildlife.

DNA vaccines deliver a portion of the pathogen's genome to the host. DNA vaccination has been successfully adapted and licensed for horses against West Nile virus (Davis et al., 2001). These vaccines have the advantage of being inexpensive to produce, the capacity to be readily ramped up to generate large quantities of vaccine, and are currently being tested in humans (Jin et al., 2015). Bison have been tested using DNA vaccines for brucellosis (Clapp et al., 2011). The bison white blood cells responded in a time-dependent fashion, showing that bison are responsive to DNA vaccines. Bovine calves were tested with DNA and a Semliki Forest RNA virus-vectored vaccines encoding *Brucella* superoxide dismutase (SOD) (Sáez et al., 2008). The calves responded to both vaccines as evidenced by increased antibody titers, increased T cell proliferative responses, and increased IFN- γ production. Hence, *Brucella* SOD delivered by these mechanisms was immunogenic and serves as a proof-of-concept for DNA vaccines and ruminants.

Another approach involves using *Brucella*'s outer membrane vesicles (OMVs), which tend to be highly immunogenic and often contain components that stimulate a protective immune response. Mice vaccinated with rough *B. melitensis* mutant had a 1,000-fold reduction in bacteria following a virulent *B. melitensis* challenge (Avila-Calderón et al., 2012). While not tested in a natural host for *Brucella*, the success of OMVs used in meningococcal vaccine for humans suggests this approach has potential (Carter, 2013).

To determine the efficacy of a subunit vaccine approach, additional studies are needed as many vaccine delivery systems and formulations are available to enhance the immunogenicity of these or other vaccine candidates. These studies will also need to include evaluation of adjuvants as these may selectively enhance immunity in elk and bison.

Enhancing immunogenicity. Modification of S19 or RB51 vaccines to improve immunogenicity by adding in genes that code for antigens that stimulate immune responses could be considered even though initial attempts to improve RB51's immunogenicity were successful in mice, but failed in bison and elk (Olsen et al., 2009; Nol et al., 2016). Future studies may show that more potent protective epitopes need to be expressed to confer protection in wildlife.

Remaining Gaps for Understanding and Controlling Brucellosis

5.3 DIVA Vaccines

Inclusion of a DIVA component in vaccines allows differentiation between vaccinated and infected animals. If the vaccine retains its LPS, this may produce a false positive serological response; thus, a different serological test would need to be developed to rapidly distinguish vaccinated from naturally infected animals (McGiven et al., 2015). One approach to distinguish infected from vaccinated animals is to modify a vaccine for a loss of immunoreactivity, as has been done for RB51 via the absence of O-Ag. Another such vaccine was engineered by preventing expression of the immunogenic *Brucella* protein bp26 gene, thus generating the M1-luc strain. This strain was used to vaccinate bovine calves that were challenged with virulent *B. abortus* strain 2308 (Fiorentino et al., 2008). It conferred protection against abortion similar to heifers vaccinated with S19. Subunit vaccines such as those previously described also have the advantage of not converting animals serologically, thus allowing current serological tests to be used to determine prior *Brucella* exposures and thus qualify as a DIVA.

5.4 Challenge Studies

B. abortus is classified as a biosafety level 3 (BSL-3) agent; thus, research on *B. abortus* requires the use BSL-3/ABSL-3 or higher enhanced containment conditions (BSL-3-Ag for loose-housed animals). *B. abortus* is also regulated as a Select Agent under the Bioterrorism Act of 2002, which imposes onerous registration requirements. These requirements limit the ability of researchers to conduct studies, as the Select Agent designation requires researchers to have facilities, protocols, reporting requirements, and security clearances to work with the pathogen that are beyond those required for a BSL-3 pathogen, and they are beyond the capacity of many institutions to comply. Because of the restriction, the vaccine S19 has been used as a surrogate for transmission studies in bison to understand transmission by a variety of routes (Uhrig et al., 2013). But immune responses that are important for controlling challenge with vaccine strains may differ somewhat from that needed to control infections by virulent field strains. To efficiently conduct research on immune responses to existing or new vaccines or immunotherapeutics, it will be necessary to remove *B. abortus* from the Select Agent list. A recent proposal by the USDA-APHIS to remove *Brucella* from the Select Agent list (USDA-APHIS, 2016) to reduce the restrictions on brucellosis research, although supported by the committee, was unfortunately not approved.

Standardized infection and abortion challenge methods need to be followed when conducting the vaccine trials to minimize variation among studies. This would require some initial cooperative studies to determine the minimum infection dose 100% (ID₁₀₀) for *B. abortus* for each individual to abort its first calf. A virulent *B. abortus* strain isolated from the GYA will also need to be characterized and tested in vaccine trials to determine whether *B. abortus* S2308 is the most representative strain to test. To ensure that virulence is maintained with the challenge strains, all groups will need to follow basic microbiology practices for culture and preservation. Addressing these aspects will greatly facilitate the development of more effective brucellosis vaccines to consistently protect >90% of affected wildlife and livestock against abortion and protect >85% against infection. Raising the standards of protection will effectively increase herd immunity to interrupt transmission of *B. abortus* among elk, bison, and cattle. Finally, in assessing vaccine trial outcomes, it will be necessary to address the issue of vaccines that show protection in controlled settings while they do not in field settings, and vice versa (Schurig, 2015).

6. GENOTYPING AND GENETICS

Since 1998, the accuracy and speed of DNA and RNA sequencing, “-omics” analyses, and bioinformatics have improved substantially. Variable Number of Tandem Repeat (VNTR) analysis and so-called next-generation sequencing (high-throughput sequencing) of whole genomes has allowed for a more detailed analysis of the molecular epidemiology of *B. abortus* isolates from domestic and wild ruminants (Higgins et al., 2012; Kamath et al., 2016). Research and epidemiological data have substantially changed the understanding of *Brucella* transmission from wild to domestic ruminants in the GYA, which strongly

Revisiting Brucellosis in the Greater Yellowstone Area

suggests that elk are responsible for current transmission events to domestic cattle and are a significant source of transmission to other elk and to bison (Rhyan et al., 2013; Kamath et al., 2016).

6.1 Pathogen Genotyping and Gene Expression Profiling

The profiling of *B. canis* and *Salmonella enterica* within their infected hosts resulted in the discovery of rapid genetic mutations and adaptations (Gyuranecz et al., 2013; Mather et al., 2013). A profiling analysis of *B. abortus* genomes in elk and bison in the GYA could reveal genetic differences in subpopulations of *B. abortus*. Functional adaptations within the different *Brucella* lineages may explain differences in spatial expansion. Sequencing of whole genomes is already routinely used in diagnostic testing and for molecular characterization of pathogen isolates in some laboratories. Diagnostic laboratories have used genetic differences to characterize viral and bacterial pathogens at the subspecies and isolate-specific levels. This could become a routine procedure for analyzing *B. abortus* isolates from the GYA. User-friendly and rapid formats for molecular characterization and whole genome sequencing will provide the information necessary to control brucellosis by targeting transmission pathways of specific isolates. Thus, research on molecular-based diagnostics for *B. abortus* will be needed for addressing brucellosis control in the GYA.

The use of microarrays to cover whole genome analysis of *Brucella* gene expression and the use of next-generation sequencing may enhance understanding of both host and pathogen gene expression during the infection process (Rossetti et al., 2010, 2011). *Brucella* and host gene expression and proteome datasets have been generated, progressing toward a comprehensive dual analysis of host and pathogen responses (He et al., 2010; Rossetti et al., 2010, 2013; Viadas et al., 2010; Weeks et al., 2010; Kim et al., 2013). The use of powerful bioinformatic algorithms has allowed for the analysis of datasets to identify candidate genes and biomarkers of *Brucella* and hosts, identify and predict *Brucella* antigenic proteins, identify components of subunit vaccines, understand gene regulatory networks, characterize the *Brucella* stress responses, and better understand modulation of host immune responses. The use of systems biology is needed to more effectively exploit elk and bison data for the following: (1) model development; (2) causal discovery, such as understanding the genetic basis for innate susceptibility or resistance to brucellosis; (3) prediction of biological activities, such as immune mechanisms that result in protection from disease; (4) improvement in designing *in vitro* and *in vivo* experiments to understand the biology of brucellosis; and (5) identification of biomarkers for protective immunity and diagnosis.

6.2 Host Genetic Characterization and Gene Expression Profiling

Significant advances have been made in characterizing host genetics, including sequencing of the bovine genome and substantial progress on sequencing the deer genome (red deer, *Cervus elaphus*, Rocky Mountain elk, *Cervus canadensis*) (Elsik et al., 2009; Brauning et al., 2015). Mitochondrial DNA sequencing and microsatellite analysis have enabled the bison populations within the GYA to be characterized into two distinct subpopulations (Halbert and Derr, 2008; Halbert et al., 2012). Genome analysis in cattle and water buffalo shows distinct genome markers that code for susceptibility to infection, protective immune responses, and other characteristics of genetic resistance, and the results have direct application to bison genetics (Adams and Templeton, 1998; Capparelli et al., 2007; Adams and Schutta, 2010; Martinez et al., 2010; Elsik et al., 2016). Obtaining similar data on elk genetics would allow analysis of how genotype affects vaccine efficacy. Given that infected elk are likely to abort their first calf after infection, this is likely to induce some selective pressure on elk to combat the disease more effectively and provide insight into the genetic basis for the increased resistance to *B. abortus*. Characterization of the elk genome is a priority as it may be useful as an adaptive management tool for elk in the future. Dual gene expression profiling of host and pathogen is a powerful tool to understand brucellosis infection biology (Perez-Losada et al., 2015). To identify protective brucellosis vaccine candidates, a systems biology analysis of dual *Brucella* and bovine host gene expression data were combined with reverse vaccinology; similar technological approaches could be applied to elk and bison (He and Xiang, 2010; Adams et al., 2011a,b; Chiliveru et al., 2015).

Remaining Gaps for Understanding and Controlling Brucellosis

Bison culling in the GYA has been designed to meet population targets rather than to selectively cull brucellosis-infected individuals, which has given rise to concerns about bison genetics. With currently available technology to rapidly characterize bison genetic markers and pathogen genotype in a small field-based laboratory setting, it is possible to selectively remove individuals based on disease status and specific bison genotypes. This would be a significant aid to making informed and targeted culling decisions in the bison management program and could help address the question of whether culling only infected bison will alter the “natural” population genetic structure of GYA bison.

7. DIAGNOSTICS

The success of the brucellosis eradication program in the United States is a testament to the success of the diagnostic approaches used in livestock surveillance over the past 80 years. Brucellosis detection by serology and culture has proven to be useful for both population and individual animal regulatory testing, and it has not changed appreciably since the 1998 report. These diagnostic methods will continue to be useful into the future for contact tracing if a positive cattle herd is identified in the GYA, DSAs, or immediately adjacent federal and private lands. There are logistical difficulties in capturing and retaining wild ruminant species for testing purposes that would also need to be addressed. Nevertheless, there are gaps in diagnostic testing for brucellosis in all three ruminant species that play a central role in the GYA.

7.1 Fitness for Purpose

The first step in validating assays is “fitness for purpose.” Factors taken into consideration include timeliness of results and actions arising therefrom, population versus individual animal testing, sensitivity and specificity considerations for presumptive versus confirmatory testing, DIVA, determination of infectiousness, species-specific applications, and determination of protective immunity. It may be beneficial to have diagnostic assays rapidly confirm results when testing cattle, given the history of success using the current testing algorithm as described in the Uniform Methods and Rules (UM&R) (USDA-APHIS, 2003). However, the ability to rapidly and accurately identify infected elk and to differentiate infected from vaccinated elk in the field has priority over further development of diagnostic assays for cattle, as diagnosing elk would have a significant impact on decision making when individual animals and groups of animals have been captured and/or incapacitated.

7.2 Testing Formats

Diagnostic testing technology has changed significantly since the 1998 report. The availability of both laboratory-based and pen-side testing formats has increased considerably. Assay formats in common use since the 1998 report include quantitative real time polymerase chain reaction (PCR), DIVA diagnostics, highly specific and sensitive competitive inhibition ELISA’s in kit format, chromatographic visualization such as lateral flow immunochromatography, and simplified DNA amplification techniques such as loop mediated isothermal amplification (LAMP). DNA sequencing has increased in speed and accuracy and has exponentially decreased in cost since 1998, making it a routine part of pathogen characterization in modern diagnostic laboratories.

7.3 Priorities for Diagnostic Testing Research

Improved timeliness of results and enhanced accuracy, along with better differentiation of vaccinated and infected animals using a single test, would enhance serological testing for all ruminant species that are the focus of brucellosis control in the GYA. As noted earlier, the success of the eradication program using currently available diagnostic assays for cattle suggests that improved diagnostics for cattle may not be the highest priority for development. However, if vaccine development for cattle is a research priority, it would

Revisiting Brucellosis in the Greater Yellowstone Area

be beneficial to couple any new vaccine with a DIVA diagnostic. The same priority would need to be given to coupled vaccine and DIVA diagnostic development for bison and elk.

A diagnostic test for wild ruminant diagnostics would need to be sensitive enough to avoid missing true positives, but the specificity would need to be high enough that culling of true negatives would be minimized. The required specificity for bison will likely be greater than for wild elk since genetic considerations are not as important for elk. For both of these species, it would be ideal to have field assays capable of achieving the desired level of sensitivity and specificity. Identifying bacterial DNA as a way to identify a *B. abortus* infection is challenging, particularly in individual animals. While the numbers of bacteria are extremely high in diseased tissues (e.g., aborted fetuses) and maternal birth tissues (e.g., placenta), cyclic temporal variation in the level of bacteremia is common. There will be times when bacteria are either not in the bloodstream or are at a level below the sensitivity of current PCR techniques, particularly in older individuals. Thus, false negatives are highly likely (Tiwarei et al., 2014). Nevertheless, new testing formats for PCR (such as the use of immunomagnetic beads) to concentrate bacteria prior to DNA isolation and PCR amplification can have enhanced analytical sensitivity. This technique has been successfully adapted to identify *Mycobacterium paratuberculosis*, a bacterium that can be challenging to identify by PCR from milk and feces (Khare et al., 2004).

Similarly, attempting to develop a DNA-based test to determine the infectiousness of an individual will be challenging due to the cyclic nature of the disease. A negative antigen or nucleic acid detection test result at one point in time cannot be interpreted as evidence that an individual will remain noninfectious, at least in cattle and likely in bison. Less is known about infection in elk and further studies are needed to examine the possibility that elk could have a stable carrier state in which the bacteria are at a quantity and/or located in tissue that affects transmission. Nevertheless, this is an example where caution is warranted in ensuring that the purpose of testing (e.g., determination of infectiousness) is achievable given the profile of the disease pathogenesis and the capabilities of the assay being proposed for use.

Elk diagnostic testing will become increasingly important in the future if *B. abortus* infected elk continue to spread beyond current DSAs and prevalence in elk continues to increase. While assays for testing cattle for *Brucella* infection have a long history of success in effectively identifying positive cases, none of the current diagnostic assays have optimal characteristics for rapid, sensitive, and specific determination of disease status in elk. This is due to the challenges in handling elk, obtaining specimens, and holding animals until testing is completed. Prioritization will need to be given in developing a suitable assay for serological or antigen/DNA targeted identification of infected elk, optimally in a format capable of being performed pen-side to provide reliable results in the field.

7.4 Challenges in Validating Assays for Wildlife

Obtaining positive and negative samples to validate new diagnostic tests for wildlife is difficult. Determining diagnostic sensitivity and specificity requires a large number of samples from animals with known disease status, preferably along with metadata about age, demography, stage of disease, time of year, and other similar characteristics that can impact test results. Bayesian approaches for assay validation have been used in the past by taking advantage of prior probabilities based on previous test validations, population characteristics, and other variables (Branscum et al., 2005). This approach has value when samples with a known disease status are limited. However, it would be ideal to have a biorepository of samples with associated metadata that could be accessed when a new diagnostic assay for elk or bison shows promise. The preservation of samples (e.g., serum, tissues, *B. abortus* isolates, DNA, RNA) for future host and pathogen genetic characterization in a biorepository with relevant metadata would be of significant value for research. If such a biorepository were created, it would be important to form a multi-user oversight group to manage acquisition, cataloging, and use of these valuable samples for research and diagnostic test development.

Remaining Gaps for Understanding and Controlling Brucellosis

REFERENCES

- Adams, L.G., and C.J. Schutta. 2010. Natural disease resistance to brucellosis: A review. *The Open Journal of Veterinary Science* 4:61-71.
- Adams, L.G., and J.W. Templeton. 1998. Genetic resistance to bacterial diseases of animals. *Revue Scientifique et Technique Office International des Epizooties* 17(1):200-219.
- Adams, L.G., S. Khare, S.D. Lawhon, C.A. Rossetti, H.A. Lewin, M.S. Lipton, J.E. Turse, D.C. Wylie, Y. Bai, and K.L. Drake. 2011a. Enhancing the role of veterinary vaccines reducing zoonotic diseases of humans: Linking systems biology with vaccine development. *Vaccine* 29(41):7197-7206.
- Adams, L.G., S. Khare, S.D. Lawhon, C.A. Rossetti, H.A. Lewin, M.S. Lipton, J.E. Turse, D.C. Wylie, Y. Bai, and K.L. Drake. 2011b. Multi-comparative systems biology analysis reveals time-course biosignatures of in vivo bovine pathway responses to *B.melitensis*, *S.enterica* Typhimurium and *M.avium paratuberculosis*. *BMC Proceedings* 5(Suppl. 4):S6.
- Ahmad, O.B., C. Boschi-Pinto, A.D. Lopez, C.J.L. Mur, R. Lozano, and M. Inoue. 2001. Age Standardization of Rates: A New WHO Standard. GPE Discussion Paper Series No. 31, EIP/GPE/EBD. Geneva, Switzerland: World Health Organization.
- al-Khalaf, S.A., B.T. Mohamad, and P. Nicoletti. 1992. Control of brucellosis in Kuwait by vaccination of cattle, sheep and goats with *Brucella abortus* strain 19 or *Brucella melitensis* strain Rev. 1. *Tropical Animal Health and Production* 24(1):45-49.
- Anderson, T.D., and N.F. Cheville. 1986. Ultrastructural morphometric analysis of *Brucella abortus*-infected trophoblasts in experimental placentitis. Bacterial replication occurs in rough endoplasmic reticulum. *American Journal of Pathology* 124(2):226-237.
- Araya, L.N., and A.J. Winter. 1990. Comparative protection of mice against virulent and attenuated strains of *Brucella abortus* by passive transfer of immune T cells or serum. *Infection and Immunology* 58(1):254-256.
- Araya, L.N., P.H. Elzer, G.E. Rowe, F.M. Enright, and A.J. Winter. 1989. Temporal development of protective cell-mediated and humoral immunity in BALB/c mice infected with *Brucella abortus*. *Journal of Immunology* 143(10):3330-3337.
- Arenas-Gamboa, A.M., T.A. Ficht, D.S. Davis, P.H. Elzer, A. Wong-Gonzalez, and A.C. Rice-Ficht. 2009a. Enhanced immune response of red deer (*Cervus elaphus*) to live RB51 vaccine strain using composite microspheres. *Journal of Wildlife Diseases* 45:165-173.
- Arenas-Gamboa, A.M., T.A. Ficht, D.S. Davis, P.H. Elzer, M. Kahl-McDonagh, A. Wong-Gonzalez, and A.C. Rice-Ficht. 2009b. Oral vaccination with microencapsulated strain 19 vaccine confers enhanced protection against *Brucella abortus* strain 2308 challenge in red deer (*Cervus elaphus elaphus*). *Journal of Wildlife Diseases* 45:1021-1029.
- Avila-Calderón, E.D., A. Lopez-Merino, N. Jain, H. Peralta, E.O. López-Villegas, N. Sriranganathan, S.M. Boyle, S. Witonsky, and A. Contreras-Rodríguez. 2012. Characterization of outer membrane vesicles from *Brucella melitensis* and protection induced in mice. *Clinical and Developmental Immunology* 2012:352493.
- Avila-Calderon, E.D., A. Lopez-Merino, N. Sriranganathan, S.M. Boyle, and A. Contreras-Rodríguez. 2013. A history of the development of *Brucella* vaccines. *BioMed Research International* 2013:743509.
- Belyakov, I.M., and J.D. Ahlers. 2009. What role does the route of immunization play in the generation of protective immunity against mucosal pathogens? *Journal of Immunology* 183:6883-6892.
- Branscum, A.J., I.A. Gardner, and W.O. Johnson. 2005. Estimation of diagnostic-test sensitivity and specificity through Bayesian modeling. *Preventive Veterinary Medicine* 68(2-4):145-163.
- Brauning, R., P.J. Fisher, A.F. McCulloch, R.J. Smithies, J.F. Ward, M.J. Bixley, C.T. Lawley, S.J. Rowe, and J.C. McEwan. 2015. Utilization of high throughput genome sequencing technology for large scale single nucleotide polymorphism discovery in red deer and Canadian elk. *Proceedings of the Cold Spring Harbor Laboratory*. Available online at <http://biorxiv.org/content/early/2015/11/04/027318> (accessed January 12, 2017).
- Callahan, M.K., C.R. Flaherty, and M.A. Postow. 2016. Checkpoint blockade for the treatment of advanced melanoma. Pp. 231-250 in *Melanoma*. H.L. Kaufman and J.M. Mehnert, eds. *Cancer Treatment and Research* Vol. 167. Springer.
- Capparelli, R., F. Alfano, M.G. Amoroso, G. Borriello, D. Fenizia, A. Bianco, S. Roperto, F. Roperto, and D. Iannelli. 2007. Protective effect of the Nrp1 BB genotype against *Brucella abortus* in the water buffalo (*Bubalus bubalis*). *Infection and Immunology* 75(2):988-996.
- Carter, N.J. 2013. Multicomponent meningococcal serogroup B vaccine (4CMenB; Bexsero®): A review of its use in primary and booster vaccination. *BioDrugs* 27:263-274.

Revisiting Brucellosis in the Greater Yellowstone Area

- Chen, T.H., and S.S. Elberg. 1969. Immunization against *Brucella* infections: serological and immunological studies on a soluble antigen from *Brucella melitensis*. *Journal of Infectious Diseases* 120(2):143-152.
- Chiliveru, S., M. Appari, and P. Suravajhala. 2015. On *Brucella* pathogenesis: Looking for the unified challenge in systems and synthetic biology. *Systems and Synthetic Biology* 9(1-2):73-75.
- Clapp, B., N. Walters, T. Thornburg, T. Hoyt, X. Yang, and D.W. Pascual. 2011. DNA vaccination of bison to brucellar antigens elicits elevated antibody and IFN-gamma responses. *Journal of Wildlife Diseases* 47(3):501-510.
- Clapp, B., X. Yang, T. Thornburg, N. Walters, and D.W. Pascual. 2016. Nasal vaccination stimulates CD8⁺ T cells for potent protection against mucosal *Brucella melitensis* challenge. *Immunology and Cell Biology* 34:5290-5297.
- Cross, P.C., W.H. Edwards, B.M. Scurlock, E.J. Maichak, and J.D. Rogerson. 2007. Effects of management and climate on elk brucellosis in the Greater Yellowstone Ecosystem. *Ecological Applications* 17(4):957-964.
- Davis, B.S., G.J. Chang, B. Cropp, J.T. Roehrig, D.A. Martin, C.J. Mitchell, R. Bowen, and M.L. Bunning. 2001. West Nile virus recombinant DNA vaccine protects mouse and horse from virus challenge and expresses in vitro a noninfectious recombinant antigen that can be used in enzyme-linked immunosorbent assays. *Journal of Virology* 75:4040-4047.
- Dorneles, E.M., A. Teixeira-Carvalho, M.S. Araújo, G.K. Lima, O.A. Martins-Filho, N. Sriranganathan, and A.P. Lage. 2014. T lymphocytes subsets and cytokine pattern induced by vaccination against bovine brucellosis employing S19 calfhood vaccination and adult RB51 revaccination. *Vaccine* 32:6034-6038.
- Edmonds, M.D., L.E. Samartino, P.G. Hoyt, S.D. Hagius, J.V. Walker, F.M. Enright, G.G. Schurig, and P. Elzer. 2001. Oral vaccination of sexually mature pigs with *Brucella abortus* vaccine strain RB51. *American Journal of Veterinary Research* 62:1328-1331.
- Elsik, C.G., R.L. Tellam, K.C. Worley, R.A. Gibbs, D.M. Muzny, G.M. Weinstock, D.L. Adelson, E.E. Eichler, L. Elnitski, R. Guigo, D.L. Hamernik, S.M. Kappes, H.A. Lewin, D.J. Lynn, F.W. Nicholas, A. Reymond, M. Rijnkels, L.C. Skow, E.M. Zdobnov, L. Schook, J. Womack, T. Alioto, S.E. Antonarakis, A. Astashyn, C.E. Chapple, H.C. Chen, J. Chrast, F. Camara, O. Ermolaeva, C.N. Henrichsen, W. Hlavina, Y. Kapustin, B. Kiryutin, P. Kitts, F. Kokocinski, M. Landrum, D. Maglott, K. Pruitt, V. Sapozhnikov, S.M. Searle, V. Solovyev, A. Souvorov, C. Ucla, C. Wyss, J.M. Anzola, D. Gerlach, E. Elhaik, D. Gaur, J.T. Reese, R.C. Edgar, J.C. McEwan, G.M. Payne, J.M. Raison, T. Junier, E.V. Kriventseva, E. Eyras, M. Plass, R. Donthu, D.M. Larkin, J. Reecy, M.Q. Yang, L. Chen, Z. Cheng, C.G. Chitko-McKown, G.E. Liu, L.K. Matukumalli, J. Song, B. Zhu, D.G. Bradley, F.S. Brinkman, L.P. Lau, M.D. Whiteside, A. Walker, T.T. Wheeler, T. Casey, J.B. German, D.G. Lemay, N.J. Maqbool, A.J. Molenaar, S. Seo, P. Stothard, C.L. Baldwin, R. Baxter, C.L. Brinkmeyer-Langford, W.C. Brown, C.P. Childers, T. Connelley, S.A. Ellis, K. Fritz, E.J. Glass, C.T. Herzig, A. Iivanainen, K.K. Lahmers, A.K. Bennett, C.M. Dickens, J.G. Gilbert, D.E. Hagen, H. Salih, J. Aerts, A.R. Caetano, B. Dalrymple, J.F. Garcia, C.A. Gill, S.G. Hiendleder, E. Memili, D. Spurlock, J.L. Williams, L. Alexander, M.J. Brownstein, L. Guan, R.A. Holt, S.J. Jones, M.A. Marra, R. Moore, S.S. Moore, A. Roberts, M. Taniguchi, R.C. Waterman, J. Chacko, M.M. Chandrabose, A. Cree, M.D. Dao, H.H. Dinh, R.A. Gabisi, S. Hines, J. Hume, S.N. Jhangiani, V. Joshi, C.L. Kovar, L.R. Lewis, Y.S. Liu, J. Lopez, M.B. Morgan, N.B. Nguyen, G.O. Okwuonu, S.J. Ruiz, J. Santibanez, R.A. Wright, C. Buhay, Y. Ding, S. Dugan-Rocha, J. Herdandez, M. Holder, A. Sabo, A. Egan, J. Goodell, K. Wilczek-Boney, G.R. Fowler, M.E. Hitchens, R.J. Lozado, C. Moen, D. Steffen, J.T. Warren, J. Zhang, R. Chiu, J.E. Schein, K.J. Durbin, P. Havlak, H. Jiang, Y. Liu, X. Qin, Y. Ren, Y. Shen, H. Song, S.N. Bell, C. Davis, A.J. Johnson, S. Lee, L.V. Nazareth, B.M. Patel, L.L. Pu, S. Vattathil, R.L. Williams, Jr., S. Curry, C. Hamilton, E. Sodergren, D.A. Wheeler, W. Barris, G.L. Bennett, A. Eggen, R.D. Green, G.P. Harhay, M. Hobbs, O. Jann, J.W. Keele, M.P. Kent, S. Lien, S.D. McKay, S. McWilliam, A. Ratnakumar, R.D. Schnabel, T. Smith, W.M. Snelling, T.S. Sonstegard, R.T. Stone, Y. Sugimoto, A. Takasuga, J.F. Taylor, C.P. Van Tassell, M.D. Macneil, A.R. Abatepaulo, C.A. Abbey, V. Ahola, I.G. Almeida, A.F. Amadio, E. Anatriello, S.M. Bahadue, F.H. Biase, C.R. Boldt, J.A. Carroll, W.A. Carvalho, E.P. Cervelatti, E. Chacko, J.E. Chapin, Y. Cheng, J. Choi, A.J. Colley, T.A. de Campos, M. De Donato, I.K. Santos, C.J. de Oliveira, H. Deobald, E. Devinoy, K.E. Donohue, P. Dovc, A. Eberlein, C.J. Fitzsimmons, A.M. Franzin, G.R. Garcia, S. Genini, C.J. Gladney, J.R. Grant, M.L. Greaser, J.A. Green, D.L. Hadsell, H.A. Hakimov, R. Halgren, J.L. Harrow, E.A. Hart, N. Hastings, M. Hernandez, Z.L. Hu, A. Ingham, T. Iso-Touru, C. Jamis, K. Jensen, D. Kapetis, T. Kerr, S.S. Khalil, H. Khatib, D. Kolbehdari, C.G. Kumar, D. Kumar, R. Leach, J.C. Lee, C. Li, K.M. Logan, R. Malinverni, E. Marques, W.F. Martin, N.F. Martins, S.R. Maruyama, R. Mazza, K.L. McLean, J.F. Medrano, B.T. Moreno, D.D. More, C.T. Muntean, H.P. Nandakumar, M.F. Nogueira, I. Olsaker, S.D. Pant, F. Panzitta, R.C. Pastor, M.A. Poli, N. Poslusny, S. Rachagani, S. Ranganathan, A. Razpet, P.K. Riggs, G. Rincon, N. Rodriguez-Osorio, S.L. Rodriguez-Zas, N.E. Romero, A. Rosenwald, L. Sando, S.M. Schmutz, L. Shen, L.

Remaining Gaps for Understanding and Controlling Brucellosis

- Sherman, B.R. Southey, Y.S. Lutzow, J.V. Sweedler, I. Tammen, B.P. Telugu, J.M. Urbanski, Y.T. Utsunomiya, C.P. Verschoor, A.J. Waardenberg, Z. Wang, R. Ward, R. Weikard, T.H. Welsh, Jr., S.N. White, L.G. Wilming, K.R. Wunderlich, J. Yang, and F.Q. Zhao. 2009. The genome sequence of taurine cattle: A window to ruminant biology and evolution. *Science* 324(5926):522-528.
- Elsik, C.G., D.R. Unni, C.M. Diesh, A. Tayal, M.L. Emery, H.N. Nguyen, and D.E. Hagen. 2016. Bovine Genome Database: New tools for gleaning function from the *Bos taurus* genome. *Nucleic Acids Research* 44(D1):D834-D839.
- Elzer, P.H., F.M. Enright, L. Colby, S.D. Hagius, J.V. Walker, M.B. Fatemi, J.D. Kopeck, V.C.J. Beal, and G.G. Schurig. 1998. Protection against infection and abortion induced by virulent challenge exposure after oral vaccination of cattle with *Brucella abortus* strain RB51. *American Journal of Veterinary Research* 59:1575-1578.
- Ezenwa, V.O., and A.E. Jolles. 2015. Opposite effects of anthelmintic treatment on microbial infection at individual versus population scales. *Science* 347(6218):175-177.
- Fiorentino, M.A., E. Campos, S. Cravero, A. Arese, F. Paolicchi, C. Campero, and O. Rossetti. 2008. Protection levels in vaccinated heifers with experimental vaccines *Brucella abortus* M1-luc and INTA 2. *Veterinary Microbiology* 132:302-311.
- Giauffret, A., and R. Sanchis. 1974. Etude d'un foyer d'épididymite contagieuse du bélier: Eradication de la maladie. *Bulletin-Office International Des Epizooties* 82:581-589.
- Goenka, R., M.A. Parent, P.H. Elzer, and C.L. Baldwin. 2011. B cell-deficient mice display markedly enhanced resistance to the intracellular bacterium *Brucella abortus*. *Journal of Infectious Diseases* 203(8):1136-1146.
- Gude, P.H., A.J. Hansen, R. Rasker, and B. Maxwell. 2006. Rates and drivers of rural residential development in the Greater Yellowstone. *Landscape and Urban Planning* 77:131-151.
- Gyuranecz, M., B.D. Rannals, C.A. Allen, S. Janosi, P.S. Keim, and J.T. Foster. 2013. Within-host evolution of *Brucella canis* during a canine brucellosis outbreak in a kennel. *BMC Veterinary Research* 9:76.
- Haggerty, J.H., and W.R. Travis. 2006. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 37:816-830.
- Halbert, N.D., and J.N. Derr. 2008. Patterns of genetic variation in US federal bison herds. *Molecular Ecology* 17(23):4963-4977.
- Halbert, N.D., P.J.P. Gogan, P.W. Hedrick, J.M. Wahl, and J.N. Derr. 2012. Genetic population substructure in bison at Yellowstone National Park. *Journal of Heredity* 103(3):360-370.
- He, Y., and Z. Xiang. 2010. Bioinformatics analysis of *Brucella* vaccines and vaccine targets using VIOLIN. *Immunome Research* 6(Suppl. 1):S5.
- He, Y., S. Sun, H. Sha, Z. Liu, L. Yang, Z. Xue, H. Chen, and L. Qi. 2010. Emerging roles for XBP1, a sUPeR transcription factor. *Gene Expression* 15(1):13-25.
- Higgins, J., T. Stuber, C. Quance, W.H. Edwards, R.V. Tiller, T. Linfield, J. Rhyan, A. Berte, and B. Harris. 2012. Molecular epidemiology of *Brucella abortus* isolates from cattle, elk, and bison in the United States, 1998 to 2011. *Applied and Environmental Microbiology* 78(10):3674-3684.
- Hines, A.M., V.O. Ezenwa, P.C. Cross, and J.D. Rogerson. 2007. Effects of supplemental feeding on gastrointestinal parasite infection in elk (*Cervus elaphus*): Preliminary observations. *Veterinary Parasitology* 148(3-4):350-355.
- Jacobson, J.M., L. Zheng, C.C. Wilson, P. Tebas, R.M. Matining, M.A. Egan, J. Eldridge, A. L. Landay, D.B. Clifford, A.F. Luetkemeyer, J. Tiu, A.L. Martinez, J. Janik, T.A. Spitz, J. Hural, J. McElrath, and N. Frahm. 2016. The safety and immunogenicity of an Interleukin-12-enhanced multiantigen DNA vaccine delivered by electroporation for the treatment of HIV-1 infection. *Journal of Acquired Immune Deficiency Syndromes* 71(2):163-171.
- Januszewski, M.C., S.C. Olsen, R.G. McLean, L. Clark, and J.C. Rhyan. 2001. Experimental infection of nontarget species of rodents and birds with *Brucella abortus* strain RB51 vaccine. *Journal of Wildlife Diseases* 37:532-537.
- Jiang, X., and C.L. Baldwin. 1993. Effects of cytokines on intracellular growth of *Brucella abortus*. *Infection and Immunology* 61(1):124-134.
- Jimenez de Bagues, M.P., C.M. Marin, and J.M. Blasco. 1991. Effect of antibiotic therapy and strain-19 vaccination on the spread of *Brucella melitensis* within an infected dairy herd. *Preventive Veterinary Medicine* 11:17-24.
- Jin, X., C. Morgan, X. Yu, S. DeRosa, G.D. Tomaras, D.C. Montefiori, J. Kublin, L. Corey, and M.C. Keefer. 2015. Multiple factors affect immunogenicity of DNA plasmid HIV vaccines in human clinical trials. *Vaccine* 33:2347-2353.

Revisiting Brucellosis in the Greater Yellowstone Area

- Kamath, P., J. Foster, K. Drees, C. Quance, G. Luikart, N. Anderson, P. Clarke, E. Cole, W. Edwards, J. Rhyan, J. Treanor, R. Wallen, S. Robbe-Austerman, and P. Cross. 2016. Whole genome sequencing reveals brucellosis transmission dynamics among wildlife and livestock of the Greater Yellowstone Ecosystem. *Nature Communications* 7:11448.
- Kauffman, M.E., B.S. Rashford, and D.E. Peck. 2012. Unintended consequences of bovine brucellosis management on demand for elk hunting in northwestern Wyoming. *Human-Wildlife Interactions* 6:12-29.
- Khare, S., T.A. Ficht, R.L. Santos, J. Romano, A.R. Ficht, S. Zhang, I.R. Grant, M. Libal, D. Hunter, and L.G. Adams. 2004. Rapid and sensitive detection of *Mycobacterium avium subsp. paratuberculosis* in bovine milk and feces by a combination of immunomagnetic bead separation-conventional PCR and real-time PCR. *Journal of Clinical Microbiology* 42(3):1075-1081.
- Kim, H.S., C.C. Caswell, R. Foreman, R.M. Roop, II, and S. Crosson. 2013. The *Brucella abortus* general stress response system regulates chronic mammalian infection and is controlled by phosphorylation and proteolysis. *Journal of Biological Chemistry* 288(19):13906-13916.
- Kuppuswamy, P.B. 1954. Chemotherapy of brucellosis in rams. *New Zealand Veterinary Journal* 2:110-113.
- Lin, C.L., H.C. Yang, and J.H. Kao. 2016. Hepatitis B virus: New therapeutic perspectives. *Liver International* 36(Suppl. 1):85-92.
- Lin, C.Y., S.J. Lin, Y.C. Yang, D.Y. Wang, H.F. Cheng, and M.K. Yeh. 2015. Biodegradable polymeric microsphere-based vaccines and their applications in infectious diseases. *Human Vaccine and Immunotherapeutics* 11:650-656.
- Loomis, J., and L. Caughlan. 2004. Economic Analysis of Alternative Bison and Elk Management Practices on the National Elk Refuge and Grand Teton National Park: A Comparison of Visitor and Household Responses. Open-File Report 2004-1305. Reston, VA: U.S. Geological Survey. Available online at <https://www.fort.usgs.gov/sites/default/files/products/publications/21073/21073.pdf> (accessed January 13, 2017).
- Marin, C.M., M.P. Jimenez de Bagues, M. Barberan, and J.M. Blasco. 1989. Efficacy of long-acting oxytetracycline alone or in combination with streptomycin for treatment of *Brucella ovis* infection of rams. *American Journal of Veterinary Research* 50(4):560-563.
- Martinez, R., S. Dunner, R. Toro, J. Tobon, J. Gallego, and J. Canon. 2010. Effect of polymorphisms in the *Slc11a1* coding region on resistance to brucellosis by macrophages in vitro and after challenge in two *Bos* breeds (Blanco Orejinegro and Zebu). *Genetics and Molecular Biology* 33(3):463-470.
- Mather, A.E., S.W. Reid, D.J. Maskell, J. Parkhill, M.C. Fookes, S.R. Harris, D.J. Brown, J.E. Coia, M.R. Mulvey, M.W. Gilmour, L. Petrovska, E. de Pinna, M. Kuroda, M. Akiba, H. Izumiya, T.R. Connor, M.A. Suchard, P. Lemey, D.J. Mellor, D.T. Haydon, and N.R. Thomson. 2013. Distinguishable epidemics of multidrug-resistant *Salmonella* Typhimurium DT104 in different hosts. *Science* 341(6153):1514-1517.
- McGiven, J., L. Howells, L. Duncombe, J. Stack, N.V. Ganesh, J. Guiard, and D.R. Bundle. 2015. Improved serodiagnosis of bovine brucellosis by novel synthetic oligosaccharide antigens representing the capping m epitope elements of *Brucella* O-polysaccharide. *Journal of Clinical Microbiology* 53(4):1204-1210.
- Milward, F.W., P. Nicoletti, and E. Hoffmann. 1984. Effectiveness of various therapeutic regimens for bovine brucellosis. *American Journal of Veterinary Research* 45(9):1825-1828.
- Montaraz, J.A., and A. J. Winter. 1986. Comparison of living and nonliving vaccines for *Brucella abortus* in BALB/c mice. *Infection and Immunology* 53(2):245-251.
- Moustafa, D., V.K. Garg, N. Jain, N. Sriranganathan, and R. Vemulapalli. 2011. Immunization of mice with gamma-irradiated *Brucella neotomae* and its recombinant strains induces protection against virulent *B. abortus*, *B. melitensis*, and *B. suis* challenge. *Vaccine* 29:784-794.
- Nelson, D.D., W.C. Davis, W.C. Brown, H. Li, D. O'Toole, and J.L. Oaks. 2010. CD8(+)/perforin(+)/WC1(-) gamma delta T cells, not CD8(+) alpha beta T cells, infiltrate vasculitis lesions of American bison (*Bison bison*) with experimental sheep-associated malignant catarrhal fever. *Veterinary Immunology and Immunopathology* 136(3-4):284-291.
- Nicoletti, P. 1984. Vaccination of cattle with *Brucella abortus* strain 19 administered by differing routes and doses. *Vaccine* 2:133-135.
- Nicoletti, P., and F.W. Milward. 1983. Protection by oral administration of *Brucella abortus* strain 19 against an oral challenge exposure with a pathogenic strain of *Brucella*. *American Journal of Veterinary Research* 44:1641-1643.
- Nicoletti, P., and A.J. Winter. 1990. The immune response to *Brucella abortus*—the cell-mediated response to infections. Pp. 83-96 in *Animal Brucellosis*. K. Nielsen, and J.R. Duncan, eds. Boston, MA: CRC Press.

Remaining Gaps for Understanding and Controlling Brucellosis

- Nicoletti, P., F.W. Milward, E. Hoffmann, and L. Altvater. 1985. Efficacy of long-acting oxytetracycline alone or combined with streptomycin in the treatment of bovine brucellosis. *Journal of American Veterinary Medical Association* 187(5):493-495.
- Nicoletti, P., R.P. Lenk, M.C. Popescu, and C.E. Swenson. 1989. Efficacy of various treatment regimens, using liposomal streptomycin in cows with brucellosis. *American Journal of Veterinary Research* 50(7):1004-1007.
- Nol, P., S.C. Olsen, J.C. Rhyan, N. Sriranganathan, M.P. McCollum, S.G. Hennager, A.A. Pavuk, P.J. Sprino, S.M. Boyle, R.J. Berrier, and M.D. Salman. 2016. Vaccination of elk (*Cervus canadensis*) with *Brucella abortus* strain RB51 overexpressing superoxide dismutase and glycosyltransferase genes does not induce adequate protection against experimental *Brucella abortus* challenge. *Frontiers in Cellular and Infection Microbiology* 6:10.
- Oliveira, S.C., and G.A. Splitter. 1995. CD8+ type 1 CD44hi CD45 RBlo T lymphocytes control intracellular *Brucella abortus* infection as demonstrated in major histocompatibility complex class I- and class II-deficient mice. *European Journal of Immunology* 25(9):2551-2557.
- Olsen, S.C., and W.S. Stoffregen. 2005. Essential role of vaccines in brucellosis control and eradication programs for livestock. *Expert Review of Vaccines* 4:915-928.
- Olsen, S.C., S.M. Boyle, G.G. Schurig, and N.N. Sriranganathan. 2009. Immune responses and protection against experimental challenge after vaccination of bison with *Brucella abortus* strain RB51 or RB51 overexpressing superoxide dismutase and glycosyltransferase genes. *Clinical and Vaccine Immunology* 16:535-540.
- Osnas, E.E., D.M. Heisey, R.E. Rolley, and M.D. Samuel. 2009. Spatial and temporal patterns of chronic wasting disease: Fine-scale mapping of a wildlife epidemic in Wisconsin. *Ecological Applications* 19(5):1311-1322.
- Pavlov, H., M. Hogarth, I.F. McKenzie, and C. Cheers. 1982. In vivo and in vitro effects of monoclonal antibody to Ly antigens on immunity to infection. *Cellular Immunology* 71(1):127-138.
- Pennock, N.D., J.D. Kedl, and R.M. Kedl. 2016. T cell vaccinology: Beyond the reflection of infectious responses. *Trends in Immunology* 37(3):170-180.
- Perez-Losada, M., E. Castro-Nallar, M.L. Bendall, R.J. Freishtat, and K.A. Crandall. 2015. Dual transcriptomic profiling of host and microbiota during health and disease in pediatric asthma. *PLOS ONE* 10(6):e0131819.
- Rhyan, J.C., P. Nol, C. Quance, A. Gertonson, J. Belfrage, L. Harris, K. Straka, and S. Robbe-Auserman. 2013. Transmission of brucellosis from elk to cattle and bison, Greater Yellowstone Area, USA, 2002-2012. *Emerging Infectious Diseases* 19(12):1992-1995.
- Roberts, T.W., D.E. Peck, and J.P. Ritten. 2012. Cattle producers' economic incentives for preventing bovine brucellosis under uncertainty. *Preventive Veterinary Medicine* 107(3-4):187-203.
- Rossetti, C.A., C.L. Galindo, H.R. Garner, and L.G. Adams. 2010. Selective amplification of *Brucella melitensis* mRNA from a mixed host-pathogen total RNA. *BMC Research Notes* 3:244.
- Rossetti, C.A., C.L. Galindo, R.E. Everts, H.A. Lewin, H.R. Garner, and L.G. Adams. 2011. Comparative analysis of the early transcriptome of *Brucella abortus*—infected monocyte-derived macrophages from cattle naturally resistant or susceptible to brucellosis. *Research in Veterinary Science* 91(1):40-51.
- Rossetti, C.A., K.L. Drake, P. Siddavatam, S.D. Lawhon, J.E. Nunes, T. Gull, S. Khare, R.E. Everts, H.A. Lewin, and L.G. Adams. 2013. Systems biology analysis of *Brucella* infected Peyer's patch reveals rapid invasion with modest transient perturbations of the host transcriptome. *PLOS ONE* 8(12):e81719.
- Ruff, S.P., D.E. Peck, C.T. Bastian, and W.E. Cook. 2016. Economics of transitioning from cow-calf-yearling operation to a stocker operation. *Journal of the ASFMRA* 55-76. Available online at <http://www.asfmra.org/wp-content/uploads/2016/06/434-Peck.pdf> (accessed January 12, 2017).
- Sáez, D., I. Guzmán, E. Andrews, A. Cabera, and A. Oñate. 2008. Evaluation of *Brucella abortus* DNA and RNA vaccines expressing Cu-Zn superoxide dismutase (SOD) gene in cattle. *Veterinary Microbiology* 129:396-403.
- Samartino, L.E., and F.M. Enright. 1993. Pathogenesis of abortion of bovine brucellosis. *Comparative Immunology, Microbiology and Infectious Diseases* 16:95-101.
- Schorr, R.A., P.M. Lukacs, and J.A. Gude. 2014. The Montana deer and elk hunting population: The importance of cohort group, license price, and population demographics on hunter retention, recruitment, and population change. *Journal of Wildlife Management* 78(5):944-952.
- Schumaker, B. 2013. Risks of *Brucella abortus* spillover in the Greater Yellowstone area. *Revue Scientifique et Technique Office International des Epizooties* 32:71-77.
- Schurig, G. 2015. History and Current Status of RB51. Presentation at the Fourth Committee Meeting on Revisiting Brucellosis in the Greater Yellowstone Area, November 10, 2015, Washington, DC.
- Sedgmen, B.J., E.N. Meeusen, and S.A. Lofthouse. 2004. Alternative routes of mucosal immunization in large animals. *Immunology and Cell Biology* 82:10-16.

Revisiting Brucellosis in the Greater Yellowstone Area

- Skeate, J.G., A.W. Woodham, M.H. Einstein, D.M. Da Silva, and W.M. Kast. 2016. Current therapeutic vaccination and immunotherapy strategies for HPV-related diseases. *Human Vaccines and Immunotherapeutics* 12(6):1418-1429.
- Stadler, T., D. Kühnert, D.A. Rasmussen, and L. du Plessis. 2014. Insights into the early epidemic spread of Ebola in Sierra Leone provided by viral sequence data. *PLOS Currents Outbreaks*. Available online at <http://currents.plos.org/outbreaks/article/insights-into-the-early-epidemic-spread-of-ebola-in-sierra-leone-provided-by-viral-sequence-data> (accessed January 12, 2017).
- Sutherland, S.S., A.G. Robertson, D.V. LeCras, G.M. Robertson, J.M. Johnston, and R.J. Evans. 1981. The effect of challenge with virulent *Brucella abortus* on beef cattle vaccinated as calves or adults with either *Brucella abortus* strain 19 or 45/20. *Australian Veterinary Journal* 57:470-472.
- Tabynov, K., B. Yespembetov, and A. Sansyzbay. 2014. Novel vector vaccine against *Brucella abortus* based on influenza A viruses expressing *Brucella* L7/L12 or Omp 16 proteins: Evaluation of protection in pregnant heifers. *Vaccine* 32:5889-5892.
- Tabynov, K., B. Yespembetov, S. Ryskeldinova, N. Zinina, Z. Kydyrbayev, Y. Kozhamkulov, D. Inkarbekov, and A. Sansyzbay. 2016. Prime-booster vaccination of cattle with an influenza viral vector *Brucella abortus* vaccine induces a long-term protective immune response against *Brucella abortus* infection. *Vaccine* 34:438-444.
- Thorne, E.T., and J.K. Morton. 1978. Brucellosis in elk. II. Clinical effects and means of transmission as determined through artificial infections. *Journal of Wildlife Diseases* 14:280-291.
- Tiwari, A., P. Afley, D.K. Sharma, C.S. Bhatnagar, B. Bhardwaj, G.P. Rai, and S. Kumar. 2014. Real-time PCR carried out on DNA extracted from serum or blood sample is not a good method for surveillance of bovine brucellosis. *Tropical Animal Health and Production* 46(8):1519-1522.
- Uhrig, S.R., P. Nol, M. McCollum, M. Salman, and J.C. Rhyan. 2013. Evaluation of transmission of *Brucella abortus* strain 19 in bison by intravaginal, intrauterine, and intraconjunctival inoculation. *Journal of Wildlife Diseases* 49(3):522-526.
- USDA-APHIS (U.S. Department of Agriculture's Animal and Plant Health Inspection Service). 2003. Brucellosis Eradication: Uniform Methods and Rules, Effective October 1, 2003. APHIS 91-45-013. Available online at https://www.aphis.usda.gov/animal_health/animal_diseases/brucellosis/downloads/umr_bovine_bruc.pdf (accessed January 6, 2017).
- USDA-APHIS. 2016. USDA Proposes Updates to Select Agents Registration List and Select Agent Regulations. January 14. Available online at https://www.aphis.usda.gov/aphis/newsroom/stakeholder-info/sa_by_date/stakeholder-announcements-2016/stakeholder-announcements-january-2016/sa-select-agents-reg (accessed January 7, 2017).
- Vershilova, P.A. 1961. The use of live vaccine for vaccination of human beings against brucellosis in the USSR. *Bulletin of World Health Organization* 24:85-89.
- Viadas, C., M.C. Rodriguez, F.J. Sangari, J.P. Gorvel, J.M. Garcia-Lobo, and I. Lopez-Goni. 2010. Transcriptome analysis of the *Brucella abortus* BvrR/BvrS two-component regulatory system. *PLOS ONE* 5(4):e10216.
- Vitry, M.A., C. De Trez, S. Goriely, L. Dumoutier, S. Akira, B. Ryffel, Y. Carlier, J.J. Letesson, and E. Muraille. 2012. Crucial role of gamma interferon-producing CD4⁺ Th1 cells but dispensable function of CD8⁺ T cell, B cell, Th2, and Th17 responses in the control of *Brucella melitensis* infection in mice. *Infection and Immunology* 80(12):4271-4280.
- Weeks, J.N., C.L. Galindo, K.L. Drake, G.L. Adams, H.R. Garner, and T.A. Ficht. 2010. *Brucella melitensis* VjbR and C12-HSL regulons: Contributions of the N-dodecanoyl homoserine lactone signaling molecule and LuxR homologue VjbR to gene expression. *BMC Microbiology* 10:167.
- WHO (World Health Organization). 2017. Recombinant vaccines for oral immunization of wildlife. Available online at <http://www.who.int/rabies/vaccines/recombinant/en> (accessed May 6, 2017).
- Winkler, R., and K. Warnke. 2013. The future of hunting: An age-period-cohort analysis of deer hunter decline. *Population and Environment* 34(4):460-480.
- Woodward, L.F., and R.L. Jasman. 1983. Comparative efficacy of an experimental S45/20 bacterin and a reduced dose of strain 19 vaccine against bovine brucellosis. *American Journal of Veterinary Research* 44:907-910.
- Yang, X., J.A. Skyberg, L. Cao, B. Clapp, T. Thornburg, and D.W. Pascual. 2013. Progress in *Brucella* vaccine development. *Frontiers in Biology* 8:60-77.
- Zhan, Y., A. Kelso, and C. Cheers. 1995. Differential activation of *Brucella*-reactive CD4⁺ T cells by *Brucella* infection or immunization with antigenic extracts. *Infection and Immunology* 63(3):969-975.
- zu Dohna, H., D.E. Peck, B.K. Johnson, A. Reeves, and B.A. Schumaker. 2014. Wildlife-livestock interactions in a western rangeland setting: Quantifying disease-relevant contacts. *Preventive Veterinary Medicine* 113(4):447-456.

Overall Findings, Conclusions, and Recommendations

1. WHAT'S NEW SINCE 1998?

Since the 1998 National Research Council (NRC) report *Brucellosis in the Greater Yellowstone Area*, 22 cattle herds and 5 privately owned bison herds in the three Greater Yellowstone Area (GYA) states (Idaho, Montana, and Wyoming) have been infected with *Brucella abortus*. During the same time period, all other states in the United States achieved and maintained brucellosis class-free status. A 2010 interim rule to regionalize brucellosis control enabled the three GYA states to create designated surveillance areas (DSAs) to monitor brucellosis in specific zones and to reduce the economic impact for non-affected zones. However, brucellosis has expanded beyond the original DSAs, requiring outward adjustment of DSA boundaries. The increase in cattle infections in the GYA, coupled with the spread in wildlife, has been alarming for producers in the area; moreover, the risk of additional spread from movement of GYA live-stock to other areas across the United States is increasing due to the lack of guidance and surveillance, with the potential for spread and significant economic impact outside the GYA.

In tracing the genetic lineage of *Brucella* across the ecosystem and among species, elk are now recognized as a primary host for brucellosis and have been found to be the major transmitter of *B. abortus* to cattle. All recent cases of brucellosis in GYA cattle are traceable genetically and epidemiologically to transmission from elk, not bison. This is one of the most significant changes in our understanding of brucellosis epidemiology in the GYA since 1998. The seroprevalence of brucellosis in elk in some regions has been increasing from what were historically low levels, and data strongly suggest that elk are able to maintain brucellosis infection within populations that have limited to no direct contact with the feedgrounds or with infected bison. Direct contact of elk with cattle is more prevalent than contact of cattle with bison. As a result, the risk of transmission events from elk to cattle may be increasing.

In contrast, there have been no cases of transmission from GYA bison to cattle in the 27 herds infected with brucellosis since 1998 despite no change in the seroprevalence of brucellosis in bison. This is likely a result of bison management practices outlined in the Interagency Bison Management Plan (IBMP) combined with fewer cattle operations in the GYA region where bison leave Yellowstone National Park (YNP).

The 1998 NRC report made eight recommendations for addressing control of brucellosis in the GYA by focusing primarily on reducing the risk of transmission from bison to cattle. The potential for progress in reducing the spread of brucellosis was based in part on the assumption that elk were incapable of maintaining brucellosis in the GYA population without transmission that occurs among elk in feedgrounds or from bison to elk within the ecosystem. As noted above, the scientific evidence no longer supports that assumption, as the current drivers of the spread of *B. abortus* in the region have changed.

Ecological changes within the GYA since 1998 have shifted the dynamics of wildlife populations. The reintroduction of wolves and increases in grizzly bear numbers have impacted the density and distribution of elk. Elk populations have expanded on the periphery of the GYA but have decreased inside YNP. The rising number of private landowners has changed how land is used around national parks, with private lands increasingly serving as refugia for elk from hunting.

With elk now viewed as the primary source for new cases of brucellosis in cattle and domestic bison, the committee concludes that brucellosis control efforts in the GYA will need to sharply focus

Revisiting Brucellosis in the Greater Yellowstone Area

on approaches that reduce transmission from elk to cattle and domestic bison (Conclusion 1). Managing wild bison within YNP and in the surrounding private and public lands to reduce the risk of transmission of *B. abortus* to domestic cattle and domestic bison has been a joint effort by the National Park Service (NPS), the U.S. Department of Agriculture (USDA), tribal members, and the three states that border YNP. These efforts have been successful. In the committee's view, a similarly unified effort is now essential to reduce transmission between elk and livestock. As noted above, infected elk populations are expanding beyond the traditionally accepted boundaries of the GYA. There is significant risk of brucellosis spreading beyond the GYA because of the uncertainty in locating infected elk and the lack of information about factors that predispose certain cattle operation to *B. abortus*. In addition, unlike with cattle and bison, there is no effective brucellosis vaccine for elk. These changes further complicate what was already a challenging problem in 1998. Now more than ever, there is a need to strategically address this expanding problem in a more coordinated and cost-effective way.

Recommendation 1: To address brucellosis in the GYA, federal and state agencies should prioritize efforts on preventing *B. abortus* transmission by elk. Modeling should be used to characterize and quantify the risk of disease transmission and spread from and among elk, which requires an understanding of the spatial and temporal processes involved in the epidemiology of the disease and economic impacts across the GYA. Models should include modern, statistically rigorous estimates of uncertainty.

2. ADOPTING AN ACTIVE ADAPTIVE MANAGEMENT APPROACH

The GYA is a large, complex ecosystem with significant spatial variation. Because the components of the ecosystem are either directly or indirectly linked to one another, any actions that are taken to control brucellosis could impact the entire ecosystem. Management actions will need to be assessed not only for their impact on reducing *B. abortus* transmission from wildlife to cattle and domestic bison but also for their impact on other valued ecosystem services and their potential impact outside of the GYA.

Adaptive management has been an accepted tool for managing wildlife populations for more than 30 years. Adaptive management was the subject of a recommendation in the 1998 report, but it was not discussed in depth. This report provides a more detailed discussion of adaptive management and its use in brucellosis control in the GYA (see Chapter 6). Adaptive management is characterized by flexible decision making and an iterative learning process for making more effective decisions. Management activities are typically conducted as hypothesis testing, the outcomes of which direct subsequent decisions and actions toward the ultimate goal. In the absence of carefully designed management actions that include experimental controls, it is difficult to determine the effectiveness of a particular practice, leading to a slower learning process.

Many brucellosis management efforts implemented since the 1998 report may appear to have taken an adaptive management approach; however, those efforts have not followed the basic tenet of employing an *active* process. More specifically, individual management actions were not designed or established to allow for scientific assessment of effectiveness, which is a central tenet of active adaptive management. A case in point is the study of *B. abortus* strain 19 (S19) vaccination of feedground elk in Wyoming. The Wyoming Game & Fish Department (WGFD) is to be commended for initiating a vaccination program on feedground elk and monitoring its effect—one of the few population-level manipulations of the elk brucellosis system. The conclusion that S19 vaccination is of marginal value in reducing seroprevalence in feedground elk (Maichak et al., 2017) has provided valuable information on the cost-effectiveness of remote vaccination where elk are concentrated and tolerant of human presence. However, had the study used *active* adaptive management, it could have led to a faster learning process and more rapid management changes. Examples of aspects that could have been improved include the use of replicate control feedgrounds starting at the initiation of the program, continuous assessment of the program's efficacy, periodic scientific peer-review throughout the process, and control of temporal changes through the cessation of vaccination in different groups of feedgrounds in different years. The committee recognizes the challenge in how political

Overall Findings, Conclusions, and Recommendations

sensitivity and funding affects flexibility of management actions, which may have been factors impacting this case study.

Recommendation 2: In making timely and data-based decisions for reducing the risk of *B. abortus* transmission from elk, federal and state agencies should use an *active* adaptive management approach that would include iterative hypothesis testing and mandated periodic scientific assessments. Management actions should include multiple, complementary strategies over a long period of time and should set goals demonstrating incremental progress toward reducing the risk of transmission from and among elk.

3. ADAPTIVE MANAGEMENT OPTIONS TO REDUCE RISK

There are a variety of adaptive management options for reducing risk of transmission from wildlife to cattle and domestic bison (see Chapters 5 and 7). **No single management approach can independently result in reducing risk to a level that will prevent transmission of *B. abortus* among wildlife and domestic species (Conclusion 2).** To consider any approach in isolation is to miss the bigger picture of a highly interconnected ecosystem and a broader understanding of various factors affecting risk that has evolved since 1998.

Some of the most promising options along with their pros and cons are discussed below. While there are knowledge gaps that limit understanding of actual risk, the options below are possible adaptive management approaches to reduce risk of *B. abortus* transmission and to inform future risk management plans. These approaches would need to be based on an integrated assessment of risk and costs, with priorities assigned based on such an assessment. However, these approaches do not necessarily need to be applied uniformly over space and time. The committee acknowledges that many of these actions are the focus of current management efforts. Others are either new or are adaptations of other efforts.

3.1 Population Reduction

Reducing the population size of cattle, bison, or elk are all likely to reduce the risk of brucellosis transmission to cattle by reducing the area of potential contact or the number of infected individuals in those areas, even if the disease prevalence in the wildlife hosts remains constant. However, each species has a constituency that would likely oppose any population reduction. Cattle may be logistically easier to control than wildlife, but state and federal managers are unable to directly modify cattle numbers and can change only some of the incentive structures for ranchers and landowners. Bison numbers and distribution are already controlled at the boundaries of YNP, which is inconsistent with the natural regulation policy of the NPS. Finally, large reductions in elk populations are unlikely to be widely supported (Peterson et al., 2006).

Elk

Reducing the elk population is an option for reducing the risk of transmission among elk, cattle, and bison. Unlike bison, transmission among elk appears to be influenced by density. **Thus, reducing elk group sizes and/or density may decrease elk seroprevalence over time and potentially decrease the risk of elk transmission (Conclusion 3).** Potential management approaches for elk population reduction include the following:

- *Hunting.* Hunting is currently used to control elk populations, with management unit population targets set as a balance of public demand and population goals. Hunting could also be used as a means of incentivizing targeted population reductions based on brucellosis risk. One option, for example, would be to increase the numbers taken by hunters to the extent possible in known high elk seroprevalence areas, particularly female elk. This option requires sufficient numbers of hunters to access those lands in a timely fashion, requires that herd seroprevalence is known, and

Revisiting Brucellosis in the Greater Yellowstone Area

would need to be linked to more intensive efforts to better establish seroprevalence estimates. Hunter-collected elk samples, as done in Idaho and Wyoming, could also be used to increase information on key populations where seroprevalence is critically important or unknown (e.g., at the boundary of DSAs). Higher quotas or more intensive hunter contact efforts could allow increased sampling, improving the previously low return and sample quality problems. A challenge of hunting as a management option is that it is imprecise, and in some cases, it may be seen as undesirable by hunters on whose cooperation it depends. Animals may move, unpredictable weather may make a targeted population inaccessible to hunters during a short hunting season, and activity may disrupt herds. Hunting may also concentrate remaining elk in areas that are not accessible to hunters, such as private land where cattle are grazed, thereby promoting an overall adverse outcome. There are inadequate data to conclusively recommend one or more of these options, as additional and ongoing assessments of the efficacy of these approaches would be needed as part of an active adaptive management approach.

- *Contraception.* A second approach that targets female elk that are at higher risk of transmission during birthing events is contraception. As previously discussed in Chapter 7, GonaCon™ is an immunocontraceptive and is one option suggested for reducing prevalence in bison. Contraception would need to be viewed as experimental in elk. But as noted above, early experimental results in bison suggest that GonaCon™ may help in significantly reducing the elk population and prevalence of brucellosis in elk. Contraception trials in elk were under way as of the writing of this report. The results of these early trials would need to be carefully evaluated to determine whether this tool holds potential as a useful means to help control brucellosis in elk.
- *Test and removal.* Test and removal has been an invaluable part of the brucellosis eradication program for domestic species. As with domestic species, test and removal in elk would need to be part of an integrated program combined with other tools such as quarantine, herd management to reduce intra-herd transmission, and vaccination. To determine whether this approach might be feasible for elk, a 5-year pilot study was conducted at the Muddy Creek feedground to analyze how test and removal of elk on feedgrounds might reduce seroprevalence of brucellosis. This project targeted female elk and was able to reduce the prevalence of brucellosis from 37% to 5% during the 5 years of the project by trapping nearly half of the female elk in the feedground and eliminating (by humane euthanasia) serologically positive females. Discontinued after 5 years, the project also demonstrated how quickly brucellosis prevalence could resurge in a population without continuing efforts. This “proof of principle” pilot project demonstrates that significant reduction of prevalence is possible in elk through test and removal of positive elk. But given the enormity of the problem in elk, the use of test and removal is limited to very specialized conditions (e.g., in reducing feedground density) as large populations appear to be able to maintain a brucellosis reservoir outside the feedgrounds. The logistics and cost of conducting the long-term test-and-removal programs required for success would be significant, even in the relative “confinement” of elk in a feedground (where they are accessible in a concentrated population but still move freely), and with the current lack of other tools (such as vaccination and spatial separation through quarantine) needed to ensure success. Its application will be effective only when used as one part of a comprehensive control strategy and in isolated or otherwise confined populations of elk that can be captured, tested, held, and removed without interaction with other infected elk or bison. Further analysis would be needed to determine the costs and benefits of this approach.

Bison

The threat of *B. abortus* transmission from bison to cattle may currently not be a concern, but bison remain an important reservoir for brucellosis. Therefore, the threat of transmission from bison to elk remains and could represent a long-term problem if elk were cleared of the disease. The committee identified the highest priority to be a focus on controlling *B. abortus* transmission from elk to cattle and domestic

Overall Findings, Conclusions, and Recommendations

bison. Further reducing the prevalence of brucellosis in bison may be desirable in the future if efforts are successful in reducing prevalence in elk. Additionally, further reducing prevalence in bison could also enhance the potential for more successful control in the future if new tools, such as an improved vaccine for bison, become available.

- *Removal of infected bison.* Population reduction alone is not likely to reduce brucellosis prevalence in bison since transmission is frequency dependent rather than density dependent. **For this reason, if reduction of brucellosis prevalence is a goal, removal of bison for population management purposes will need to target brucellosis-infected individuals whenever possible (Conclusion 4).**
- *Quarantine and relocation.* Sufficient evidence is now available to also include separation and quarantine of test negative bison as a management action, allowing for the eventual relocation of GYA bison to other bison herds (including onto tribal lands). However, there are limitations on the effectiveness of this approach toward population reduction since the time required to confirm *Brucella* negative status is prolonged, the number of bison that can be relocated is not large, and relocation sites will reach maximum carrying capacity over time.
- *Targeted removal within YNP.* While this option may not be politically, logistically, socially, or economically feasible, targeted removal of seropositive bison (which would be facilitated by the use of a pen-side assay) or high-risk bison (such as young pregnant females) within YNP in the winter could reduce the need for large culls of bison populations that move outside YNP. This could also reduce the episodic swings in the bison population and winter emigrations from YNP that lead to large culls in some years. Additionally, any gains in reducing seroprevalence in bison could be negated by exposure of remaining bison to infected elk within YNP and in elk feedgrounds if concurrent efforts to reduce seroprevalence in elk does not occur. This is particularly important for the Jackson bison herd, for which exposure to elk on the National Elk Refuge (NER) continues to be a significant risk and will need to be considered in bison control plans. However, the impact could be assessed using an active adaptive management approach.
- *Bison genetics.* Test and removal of bison provides a valuable opportunity to preserve genetic material and live cells for future use in establishing brucellosis negative and potentially disease resistant bison through cloning techniques.
- *Contraception.* Experimental and modeling results in bison suggest that contraception using a gonadotropin-releasing hormone immunocontraceptive (i.e., GonaCon™) may help in reducing prevalence of brucellosis. This approach targets high-risk females, preventing pregnancy and thus abortion and birthing events that increase risk of transmission through shedding of high numbers of bacteria. Contraception would need to be used strategically, recognizing that population reduction (an outcome of using contraception) may not be acceptable for bison in all areas.

3.2 Feedgrounds

The role of the NER and Wyoming elk supplemental winter feedgrounds in maintaining and propagating brucellosis in the GYA is a controversial topic. Feedgrounds have been useful for separating elk from cattle. However, it is widely accepted that the feedgrounds promote transmission of *B. abortus* among elk and are likely responsible for causing and maintaining elevated seroprevalence in those areas. Molecular genetic characterization of *B. abortus* isolates from elk, bison, and cattle indicate that Wyoming feedgrounds have the greatest diversity of *B. abortus* lineages, and strongly suggest that they are the initial source of infection for other elk populations in the GYA, with the exception of some isolates from the Paradise Valley in Montana.

Revisiting Brucellosis in the Greater Yellowstone Area

Feedground Interventions

The committee reviewed multiple experimental approaches to reduce elk seroprevalence by intervention in the feedgrounds. On balance, the data are not yet strong enough to make definitive conclusions on the outcome, particularly if the ultimate outcome is the reduced risk of exposure and infection rates in cattle. Decisions will need to be made that balance the short-term goals of separating elk from cattle with the long-term risk of increased infection among elk in feedgrounds. The potential options below for management interventions in feedgrounds could be further evaluated using an active adaptive management approach, with the interventions applied singularly or in combination.

- *Balance the timing and use of feedgrounds.* Data suggest that ceasing feeding earlier in the season on feedgrounds to encourage dispersal would result in less risk of infection among elk (and bison where intermixing occurs), because calving of elk would occur in a more natural environment away from the dense population of elk that are present in feedgrounds. This approach would have to be balanced with appropriate management of cattle, with delayed turnout into grazing areas until the risk of exposure during elk calving is reduced, as well as consideration of habitat improvement for elk that would provide forage along migration routes and winter habitat to reduce elk-cattle contact in the absence of the feedgrounds.
- *Feeding patterns on feedgrounds.* Data suggest that feeding in checkerboard patterns and spreading feed more broadly appear to reduce elk-to-elk contact, and therefore potentially reduce transmission risk.
- *Test and removal on feedgrounds.* The Muddy Creek feedground pilot project provided an example of temporarily reducing seroprevalence of brucellosis through test and removal of infected female elk. The feedgrounds offer an opportunity to work with a population of elk that is seasonally concentrated. This option was discussed in detail above in the “Population Reduction” section, and as previously mentioned in that section, the test-and-removal strategy will be effective only when used as one part of a comprehensive control strategy for brucellosis.
- *Contraception in elk.* Also discussed above is the option of contraceptive intervention in elk. The feedgrounds provide an opportunity to more easily access female elk for contraceptive application.
- *Removal of aborted fetuses.* Aborted placentae pose the highest risk of exposure of uninfected elk to brucellosis since the concentration of bacteria is extremely high at the time of abortion. Access to these fetuses is more limited when elk calve in the natural environment. Abortion on feedgrounds offers an opportunity to remove aborted fetuses on a daily basis and to disinfect the abortion site using an appropriate disinfectant (such as sodium hydroxide or sodium hypochlorite), thus reducing the likelihood of transmission to other elk. Current feedground practice includes removal of aborted fetuses when identified. However, data are not sufficient to know the impact of doing this on reduction of seroprevalence in elk, and subsequently on reducing infection risk for cattle over time. Managers should continue investigating methods of reducing the amount of time aborted fetuses are on the feedground as well as the number of contacts that elk and bison (i.e., the Jackson bison herd) have with those fetuses.
- *Other future interventions.* Given the enormity of the challenge in accessing elk in the vastness of the open West, feedgrounds offer a unique opportunity to intervene (e.g., if an effective elk vaccine is developed) in a relatively smaller land area where elk are concentrated and capture is easier, less dangerous for personnel, and less costly. This potential future opportunity should be weighed against the ongoing costs and benefits of maintaining the feedgrounds in an integrated socioeconomic analysis.

*Overall Findings, Conclusions, and Recommendations**Incremental Closure of Feedgrounds*

Closure of feedgrounds appears to be an obvious approach to control brucellosis in the GYA, but there are impacts of feedground closure that will need to be considered and assessed. First, while there is still some uncertainty, scientific evidence suggests that brucellosis in elk is self-sustaining in some areas without continuous reintroduction of infected feedground elk. If future work continues to support this conclusion, it is possible that closure of feedgrounds would not have any impact on brucellosis prevalence in more remote elk populations away from the feedgrounds. Closure of feedgrounds would, however, potentially reduce the “seeding” of new areas with infected elk where a reservoir does not currently exist. Second, anecdotal evidence suggests that feedgrounds reduce exposure of cattle to infected elk during the high-risk period of abortion or calving. Observational data to support this notion are weak at present. Thus, an unintended outcome of closing feedgrounds could be increased exposure of cattle to infected elk if cattle are turned onto grazing areas at the time that elk are calving.

Feedground closure has been the subject of increased discussion due to disease concerns in addition to brucellosis. In particular, at the time of this report, the spread of chronic wasting disease (CWD) and the distinct possibility that feedgrounds will be a primary source of transmission for many years into the future has led to more active discussions on closing of feedgrounds (the role of feedgrounds in the transmission of other diseases of elk was discussed in Chapter 7). Reduced use and/or strategic closing of feedgrounds may have a positive impact on elk health in general, although the data supporting the trade-off of increased winter population loss with reduced disease impacts on overall elk population (measured, for example, in terms of number of cow-calf pairs) are unclear. The committee was not tasked to review the role of feedgrounds in propagation of CWD in elk but notes that the concern is supported by scientific evidence.

There are insufficient data available to know with certainty what the impact across the entire GYA would be of reducing the use of and possibly closing elk supplemental feedgrounds. However, **the weight of evidence nonetheless suggests that reduced use or incremental closure of feedgrounds could benefit elk health in the long term and could reduce the overall prevalence of brucellosis in elk on a broad population basis (Conclusion 5).**

The closure of feedgrounds is likely to bring increased short-term risk due to the potential for increased elk-cattle contact while the seroprevalence in elk remains high. In the longer term, closing feedgrounds may result in reduced elk seroprevalence. Incremental closure of feedgrounds would enable a bio-economic assessment to be conducted to determine both short- and long-term costs and benefits. **Reduced use or incremental closure of feedgrounds is not a stand-alone solution to control of brucellosis in the GYA and will need to be coupled with other management actions to address the problem at a systems level (Conclusion 6).** The committee endorses the long-term goal presented in the WGFD Brucellosis Management Action Plans and the USFWS-NPS elk and bison management plan for the NER to reduce use and/or incrementally close supplemental feedgrounds.

Recommendation 3: Use of supplemental feedgrounds should be gradually reduced. A strategic, stepwise, and science-based approach should be undertaken by state and federal land managers to ensure that robust experimental and control data are generated to analyze and evaluate the impacts of feedground reductions and incremental closure on elk health and populations, risk of transmission to cattle, and brucellosis prevalence.

3.3 Spatial and Temporal Separation

One of the fundamental principles of infectious disease control is spatial and temporal separation of individuals and groups to reduce the risk of transmission. This principle underlies progress made in reducing bison and cattle contact outside YNP as part of the IBMP. Bison management to prevent brucellosis transmission has been successful in part due to spatial and temporal separation from cattle, both because bison are largely contained within YNP and the Grand Teton National Park and, when outside the parks,

Revisiting Brucellosis in the Greater Yellowstone Area

they are managed to reduce cattle contact. In addition, a relatively small and decreasing number of cattle are grazed close to areas where bison roam outside the park, helping to keep the risk of exposure minimal.

Recommendation 4: Agencies involved in implementing the IBMP should continue to maintain a separation of bison from cattle when bison are outside Yellowstone National Park boundaries.

Spatial and temporal separation plays an important role in reducing transmission risk from elk. Separation of susceptible and infected animals during high-risk periods (e.g., immediately prior to and following abortion and full-term birth) has been and should continue to be utilized as a risk-reduction tool and is further discussed below in the context of specific management approaches. National policy for responding to the identification of infected cattle and domestic bison herds includes time-tested approaches toward maintaining separation of infected and susceptible animals, including hold orders and quarantine during follow-up testing. These actions are valuable tools for reducing risk. Other options include the timing and use of grazing allotments, biosecurity measures, and hazing of elk. Removal of bison for population management purposes could target *B. abortus*-infected bison if further reducing the prevalence of brucellosis is a goal; however, until tools become available that would simultaneously allow for an eradication program in elk, additional aggressive control measures in bison seem unwarranted.

Grazing Allotments

At least 75% of the cattle herds infected since 1998 had previously grazed on or immediately adjacent to public rangeland. Historically, reduction of *B. abortus* transmission risk has not been considered by agencies when making decisions about assigning grazing allotments. Case-control studies along with more frequent cattle testing would be required to more definitively link public land access to brucellosis infection risk in cattle. However, a more science-based approach in grazing allotment use could be taken to reduce risk. For example, government agencies such as USDA's Forest Service and the U.S. Department of the Interior's (DOI's) Bureau of Land Management could leave grazing allotments empty or modify the use and timing of grazing allotments in relation to the risk of transmission and knowledge of elk migration patterns. Additionally, the formula used annually to adjust grazing fees could be changed to a risk-based, marketplace approach through legislative authorization. To do so would require an understanding of when and where the risks are higher and lower, and the development and use of a risk map that overlays cattle and elk locations relative to the grazing allotments. Decisions should be made in consultation with state wildlife agency partners to estimate when elk are less likely to be on federal grazing allotments during the time when abortion and calving events occur and to consider other factors that reduce the likelihood of interactions between elk and cattle on grazing allotments. Increased knowledge of elk transmission risk in grazing allotments will be critical to taking a targeted approach toward risk reduction by spatial and temporal separation. If delayed access is unacceptable to producers, increased fees and/or brucellosis testing prior to and after turnout on grazing allotments could be implemented. Requiring evidence of brucellosis calfhood and adult vaccination for grazers using higher risk lands could also be required. The benefits from this approach are somewhat uncertain due to, for example, a limited understanding of where and when cattle are getting infected (addressed later in the "Research Agenda" section). However, if designed appropriately, iterative learning through an active adaptive management approach will over time provide the data as to whether this approach is effective and worth continuing.

Biosecurity Measures

There are multiple biosecurity measures that individual producers can take that reduce exposure of cattle and domestic bison to *B. abortus*-infected elk. Measures such as fencing of haystacks and delaying turnout on summer pasture until the risk of elk calving is reduced have been discussed in the report. There are adequate data to indicate these approaches can reduce exposure, and published cost-benefit analysis has

Overall Findings, Conclusions, and Recommendations

provided the individual producer with sufficient information to make personal decisions. However, as previously discussed, the external impacts (externalities) of individual producer actions have not been thoroughly investigated. In general, actions taken by individual producers should be in proportion to the risk of elk entering their property or otherwise to the risk of their cattle making contact with elk. There is a need to approach biosecurity measures as a shared responsibility, with incentives provided to producers to implement these biosecurity measures in high-risk areas (e.g., within the DSA).

Hazing of Elk

Hazing has been used by state wildlife agencies as a key part of the bison management plan for keeping bison and cattle separated after movement of bison outside YNP. Hazing is currently being authorized as a tool for Wyoming, but the efficacy of different hazing methods to reduce the time elk spend in contact with cattle has not been measured, and therefore the costs and benefits of hazing elk are unknown. Hazing of elk could be considered on a targeted basis in known high-risk areas. The impact of hazing in high-risk areas would need to be further studied to determine if hazing was effective in preventing contact between elk and cattle, or if it simply scatters elk into new locations in an unpredictable manner.

3.4 Testing, Surveillance, and Designated Surveillance Areas

Regionalization is now a well-accepted approach to allow subnational disease containment without jeopardizing the disease status of an entire nation. The success of regionalization relies on robust risk assessment, knowledge of the location and extent of infected animals within and immediately outside the boundary of a control zone, and effective boundary management and enforcement. With the last remaining vestige of brucellosis limited to the GYA, the United States adopted a regionalized approach through a 2010 interim rule that required creation of DSAs within the three GYA states (Idaho, Montana, and Wyoming). This approach minimizes the economic impact of finding occasional “spillover” disease in GYA cattle and domestic bison herds, and it provides a means for all three of the GYA states to be classified as “free” of brucellosis. The DSA zoning concept is a valuable approach toward brucellosis control in the GYA. The successful use of DSAs is dependent on responsible and timely adjustments of DSA boundaries based on adequate surveillance, particularly of elk.

There is no federal guidance for conducting wildlife surveillance outside of the DSA at a level required to monitor the geographic expansion of brucellosis in elk. Each state independently conducts wildlife surveillance outside of the DSA, with no uniform data-based guidelines or requirements for states to reference in determining when to expand their DSA as a result of finding infected or exposed wildlife outside of established DSA boundaries. This lack of uniformity in rules and standards has resulted in an uneven approach to surveillance and to establishing boundaries that accurately reflect risk. No infected cattle herds have been identified outside of established DSA boundaries, an indication that the DSA concept is effective in preventing movement of infected livestock outside of the DSA. However, seropositive elk have been identified outside of DSAs. It is therefore likely that cattle in the same geographic area are at risk. If DSA boundaries are not expanded in a timely manner in response to finding seropositive wildlife, there is an increased probability that exposed or infected cattle and domestic bison herds in that area may not be detected in time to prevent further spread of infection as cattle and domestic bison are marketed and moved.

Further raising the risk of brucellosis spread outside DSAs is a gap in slaughter surveillance for non-DSA cattle in the GYA states. There is no major slaughter capacity in Montana or Wyoming where surveillance samples can be collected to detect whether brucellosis has expanded in cattle beyond the DSA boundaries. In addition, the current national brucellosis slaughter surveillance program is not designed specifically to address the increased surveillance needs in the GYA or associated states. This gap in slaughter surveillance for non-DSA cattle in the three GYA states further raises the risk of brucellosis spreading beyond DSAs. Last, USDA’s Animal and Plant Health Inspection Service (APHIS) has not reviewed Brucellosis Management Plans for GYA states since 2012.

Revisiting Brucellosis in the Greater Yellowstone Area

The lack of data-based guidance and uniformity in conducting wildlife surveillance outside the DSA, the absence of a GYA-focused approach for national surveillance, and the infrequent oversight of state brucellosis management plans in the midst of expanding seroprevalence of the elk has increased the risk for spread of brucellosis in cattle and domestic bison outside the DSA boundaries and beyond the GYA (Conclusion 7). The impact of brucellosis spread could be substantial.

Recommendation 5: In response to an increased risk of brucellosis transmission and spread beyond the GYA, USDA-APHIS should take the following measures:

5A: Work with appropriate wildlife agencies to establish an elk surveillance program that uses a modeling framework to optimize sampling effort and incorporates multiple sources of uncertainty in observation and biological processes.

5B: Establish uniform, risk-based standards for expanding the DSA boundaries in response to finding seropositive wildlife. The use of multiple concentric DSA zones with, for example, different surveillance, herd management, biosecurity, testing, and/or movement requirements should be considered based on differing levels of risk, similar to current disease outbreak response approaches.

5C: Revise the national brucellosis surveillance plan to include and focus on slaughter and market surveillance streams for cattle in and around the GYA.

3.5 Vaccination

Vaccination is a time-tested, proven method of infectious disease control. Brucellosis vaccination has been an important part of the program to eradicate brucellosis from domestic cattle and is effective when used in conjunction with other disease management approaches such as quarantine, herd management to reduce intra-herd transmission, and test and removal. However, all 22 infected cattle herds identified since the 1998 report were at minimum official calfhood vaccinated herds, including some that were calfhood and adult vaccinated. It is important to note that direct exposure to a high infectious dose of the bacteria (e.g., through direct contact with aborted fetus and placenta) can reduce the protective benefit of the vaccine. Therefore, while it is not appropriate based on these data to conclude that vaccination is an ineffective management tool to prevent infection, it illustrates the need for vaccines to be combined with other management approaches in control programs. Vaccination does have a role in preventing further transmission by significantly reducing abortions, which is considered a very high-risk event with regard to transmission among cattle.

An improved vaccine for each of the three species (elk, bison, and cattle) would help suppress and eventually eliminate brucellosis in the GYA. For free-ranging bison and elk, appropriate and cost-effective vaccine delivery systems would be critical. Rabies vaccination of wildlife and domestic animals is a classic example of successful vaccination campaigns to protect public health, domestic animal health, and wildlife health. It has been used very effectively in North America for reducing prevalence in domestic dogs to near zero using traditional vaccines. Species-specific vaccine-laden baits have also been used to greatly reduce disease in wildlife (fox, skunk, and raccoon) and thus reduce exposure risk to humans and domestic animals. Relevant to a national park, the opposite approach has been used in Tanzania where a “ring” vaccination approach around Serengeti National Park is used very effectively to control rabies transmission from domestic dogs outside the park to wildlife within the park. But even use of a highly effective vaccine for immunization of cattle in and around the GYA would not be the solution to brucellosis management in the GYA unless coupled with an effective vaccine for elk or other means to prevent further expansion of *B. abortus*-infected elk outside current DSA boundaries. However, until the issue of infected elk transmitting *B. abortus* to cattle is fully addressed, there will still be a perception of risk by other states that will likely drive continued brucellosis testing of cattle leaving DSAs even if cattle are vaccinated with a highly effective vaccine. Nevertheless, the committee concludes that **the significant reduction in risk of transmission among vaccinated cattle provides sufficient reason to continue calfhood and adult vaccination of high-risk cattle when coupled with other risk reduction approaches (Conclusion 8).**

*Overall Findings, Conclusions, and Recommendations***4. BIOECONOMICS: A FRAMEWORK FOR MAKING DECISIONS**

Economic resources for managing disease risks in the GYA are scarce. Any management strategies that impose costs on agencies and other stakeholders while producing few to no benefits will not be adopted. Costs are not limited to direct monetary costs of undertaking management actions, and benefits are not limited to reduced economic risks to cattle producers; the costs and benefits also include the positive and negative impacts to the ecological processes of the region that are valued (either directly or indirectly) by stakeholder groups. Moreover, many costs and benefits ultimately depend on how individual ranchers, landowners, and resource users respond to changes in risk. Many of these benefits and costs will not be realized in the short term, and thus a long-term perspective and clearly communicating that perspective are needed in managing the entire system.

A significant change since the 1998 report has been the development of systems-level approaches to solving coupled socioeconomic, biological, and ecological problems. It is now common to find multidisciplinary teams of scientists involved in addressing some of society's most complex problems that are particularly difficult to solve because of their interactions with multiple underlying factors that are changing or not well understood. Brucellosis control in the GYA is a prime example of such a problem, and can benefit from a systems-level approach. **Bioeconomic modeling provides a valuable framework for systems-level decision making that is able to take into account the socioeconomic costs and benefits of reducing transmission from wildlife to domestic cattle and bison and is able to promote coordination and targeting of actions spatially and temporally based on expected costs and benefits, including potential impacts beyond the GYA.**

Quantitative models that include short- and long-term epidemiological and economic risks can help managers decide how to target resources to activities based on the costs and benefits of those activities. Part of this framework includes a periodic, performance-based evaluation of effectiveness. It would also be important to tie the allocation of public financial resources to risk reducing behaviors.

While the Statement of Task requests a cost-benefit analysis for various management options, **a lack of critical information severely limits the ability to develop a comprehensive empirical assessment at this time.** There are significant knowledge gaps for key economic and disease ecology relations, including the effectiveness, cost, and unanticipated impacts of various candidate management options to control brucellosis in the broader GYA system. Given this and other considerations, a benefit-cost assessment with specific, quantified results to guide prescriptive actions is beyond the scope of this report. Even though it may take some time to develop a bioeconomic model, such a model will be essential for decision makers in managing scarce resources to determine the most appropriate and cost-effective solutions. Consideration of research needs relative to closing the gaps in knowledge that limit cost-benefit analysis are considered below in the final section of this chapter (see "Research Agenda").

A coupled systems/bioeconomic framework is vital for evaluating the socioeconomic costs and benefits of reducing brucellosis in the GYA and would be needed to weigh the potential costs and benefits of particular management actions within an adaptive management setting. A bioeconomic framework is also needed to identify appropriate management actions to target spatial-temporal risks, including risks beyond the GYA (Conclusion 9).

5. A CALL TO STRATEGIC ACTION

A statement made in the 1998 report is particularly noteworthy given the increase in brucellosis in cattle in the GYA since 1998. "Because neither sufficient information nor technical capability is available to implement a brucellosis eradication program in the GYA at present, eradication as a goal is more a statement of principle than a workable program. The best that will be possible in the near future will be reduction of the risk of transmission of *B. abortus* from wildlife to cattle." The current committee similarly concurs that eradication of brucellosis from the GYA remains idealistic but is still not currently feasible for multiple scientific, social, political, and economic reasons. The term "eradication" denotes a complete absence of a disease agent, in this case within the GYA, and is distinct from "elimination" of brucellosis in a

Revisiting Brucellosis in the Greater Yellowstone Area

given population such as domestic cattle. Thus, while eradication of brucellosis in the GYA remains a distant goal, significant progress toward reducing or eliminating brucellosis transmission from wildlife to domestic species is possible. Undoubtedly, sufficient societal and political will, along with sufficient financial resources, will be required for success.

Managing an ecosystem as complex as the Greater Yellowstone Ecosystem will require coordination and cooperation from multiple stakeholders and will require expertise across many disciplines to understand the intended and unintended costs and benefits of actions (Conclusion 10). Addressing brucellosis under the new and changing conditions in the region necessitates a more systematic, rigorous, and coordinated approach at several levels—from priority setting to information gathering, data sharing, and wildlife and disease management—than has occurred thus far. The current approaches are likely to remain insufficient to decrease the risk of brucellosis in the region. **A strategic plan is needed to coordinate future efforts, fill in critical knowledge and information gaps, and determine the most appropriate management actions under a decision-making framework that is flexible and accounts for risks and costs (Conclusion 11).**

5.1 Coordinating a Complex System

Management of brucellosis in the GYA is under the jurisdiction of various state, federal, private, and tribal authorities. Each entity has its own mission and goals, and at times these goals may conflict with one another. In addition, there are private landowners, hunters, and ranchers whose actions can impact and are impacted by the decisions of others. To date, the efforts undertaken by various state and federal entities have been conducted in a piecemeal fashion, resulting in a disjointed and uneven approach. Moreover, actions taken have not been effective in addressing the problem because they have not addressed the issues on a systems level. While each state has the right to establish independent management approaches, management actions within each state can have external impacts for the other two states in the GYA and beyond; similarly, each federal agency has the right to establish independent management approaches for their area of jurisdiction, yet there may be unintended consequences that impact the mission and goals of other agencies. This points to the need for a coordinated, mutually agreed upon approach among state and federal agencies charged with managing brucellosis in the GYA.

Coordinated efforts across federal, state, and tribal jurisdictions are needed, recognizing firstly that *B. abortus* in wildlife spreads without regard to political boundaries and secondly that the current spread of brucellosis will have serious future implications if it moves outside of the GYA (Conclusion 12). Future progress will depend on actions of private and public stakeholders and will require integrating multiple scientific approaches. Therefore, a greater level of transparency in management actions, data collection, and data sharing will be required at both state and federal levels to inform the actions of private and public stakeholders.

Recommendation 6: All federal, state, and tribal agencies with jurisdiction in wildlife management and in cattle and domestic bison disease control should work in a coordinated, transparent manner to address brucellosis in multiple areas and across multiple jurisdictions. Effectiveness is dependent on political will, a respected leader who can guide the process with goals, timelines, measured outcomes, and a sufficient budget for quantifiable success. Therefore, participation of leadership at the highest federal (Secretary) and state (Governor) levels—for initiating and coordinating agency and stakeholder discussions and actions and in sharing information—is critical.

5.2 Integration of Management Approaches

Historically, there was great interest in brucellosis at the highest levels of government through the Greater Yellowstone Interagency Brucellosis Committee (GYIBC). GYIBC functioned effectively for a number of years, but its success ultimately suffered from a lack of authority to mandate changes across the region. While the threat has expanded since 1998, the participation of essential stakeholders has diminished

Overall Findings, Conclusions, and Recommendations

due to loss of interest caused by lack of a positive outcome or productive movement in the disease progression within the wildlife populations. There is a need to reinvigorate this interest with buy-in and participation of leadership and development of a mechanism for coordinating policy and management actions. This coordinating mechanism will need to operate under a political mandate from leadership and will need to involve all public and private entities with a stake in brucellosis control. The coordinating mechanism will need to be adequately funded and will need to operate independently to make science-based recommendations directly to leadership with the authority to implement the recommended actions. **The following considerations are critical when developing a mandate for high-level coordination:**

- Establishing goals and objectives on an ecosystem-wide basis, with performance-based measures and outcome assessment tied to funding decisions.
- Acknowledging the interrelationships of all elements of the ecosystem that requires a regional solution, with shared costs and possible redistribution of funds among agencies and states that have a stake in the outcome.
- Developing a long-term solution to managing or controlling brucellosis in the GYA that facilitates collaboration across jurisdictions (federal, state, tribal, and private).
- Developing standardized methods and rules governing the borders, operation, testing protocols, and movement requirements of the designated surveillance areas. Current methods and rules are loosely defined and specific to each state, and they do not appear to be based on a formal assessment of risk and outcomes. (Management of the designated surveillance areas was previously discussed.)
- Sharing of information and data across the tristate area to successfully control the spread of brucellosis in the GYA. As noted above, each state has the authority to approach brucellosis control independently; however, the problem requires a systems-level approach and systems-level analysis of data to assess the performance of management policies and actions.

The success of an interagency group is dependent on leadership and on its participants. Thus, it would be imperative for a federal agency with regulatory oversight of brucellosis (such as USDA) to take leadership in moving the discussions forward. One approach for harmonized policy development includes the formation of a national-level coordinating council with representation of stakeholders from all federal agency, tribal, and state jurisdictions. An example of an effective interagency group is the Coordinating Council (CC) for the National Animal Health Laboratory Network (NAHLN). The CC (originally termed a Steering Committee) is led by USDA and includes representatives from state departments of agriculture and national and state laboratories. The original Steering Committee was formed in 2002, and it drafted and recommended policies and operational protocols for the NAHLN that have withstood the test of time. The success of this approach has hinged on the participation and agreement of high-level leadership from multiple government agencies when critical and sometimes controversial issues were discussed.

5.3 Integration of Scientific Approaches

A forum to coordinate scientific approaches toward brucellosis control among all states and agencies with jurisdiction in the GYA would be a valuable mechanism to ensure that science informs policy. Such a body would share information, prioritize research projects, limit duplication of efforts, advise on management actions, and serve as a potential venue for communicating scientifically sound and agreed-upon messages and policies to the public.

The research forum established by the Wyoming Consortium for the Advancement of Brucellosis Science (CABS) serves as a good example of a setting that brings together scientists to draw conclusions based on data with the intent to inform policy decisions. Broadening the mandate of a scientific working group like CABS to include coordination of brucellosis control across the entire ecosystem would provide a valuable forum to ensure that the best available science is being considered with regard to ecological

Revisiting Brucellosis in the Greater Yellowstone Area

rather than political boundaries. A scientific working group could be advisory to a national level coordinating council, encompassing multiple scientific disciplines to include expertise in ecology, biology, infectious diseases, disease modeling, vaccines, social sciences, and economics.

As noted previously, sharing of information and data is essential for making progress on a system wide approach toward brucellosis control. It will be important to ensure that publicly funded data and other scientific information essential to informing management actions are openly and freely available. One role of the scientific working group could be in developing or recommending appropriate policies that govern open access, as an open data policy would facilitate exchange of information and data across boundaries and jurisdictions. Although some data on elk population size and seroprevalence are available, they are not available as raw data or in machine-readable formats, which makes them difficult to use. Additionally, cattle, bison, and elk space-use data are critical to understanding risk, yet they are not easily accessible to the public as privacy concerns limit the sharing of certain data on private entities. However, transparency and sharing of data for cattle, elk, and bison are important for a system-wide analysis of risk and smarter decision making based on risk. **The committee finds that the lack of openly accessible data has limited the amount of scientific progress on controlling brucellosis, slowed the learning process, and limited critical information necessary for making decisions. Unless there are legal restrictions related to privacy concerns, data should be shared across agencies and should be made more accessible (e.g., placing data online in interoperable formats or providing access to raw data).**

6. RESEARCH AGENDA

Eliminating *B. abortus* transmission within wildlife populations (elk and bison) and from wildlife to cattle and domestic bison in the GYA—and by extension, eliminating it from the United States—is not feasible unless critical knowledge gaps are addressed. An integrated, multidisciplinary approach is necessary for addressing multiple aspects of the problem; thus, research teams will need to include members from various disciplines who provide relevant expertise and understanding. This will also require collaboration and coordinated communications among the university, agency, and nonprofit research communities.

Recommendation 7: The research community should address the knowledge and data gaps that impede progress in managing or reducing risk of *B. abortus* transmission to cattle and domestic bison from wildlife. The committee identifies several knowledge gaps across various disciplines and includes a relative ranking in relation to how crucial the gaps are and how likely it would be to impact near-future management decisions. Where appropriate, the critical knowledge and data gaps are noted by species (e.g., both elk and bison are specified for some areas while only elk are noted for others). It is important to emphasize that research should be cross-disciplinary to address the problem on a systems level.

6.1 Brucellosis Disease Ecology and Cattle Risk

Recommendation 7A: Top priority should be placed on research to better understand brucellosis disease ecology and epidemiology in elk and bison, as such information would be vital in informing management decisions. Research would need to (1) identify and understand the factors driving the rate and direction of *B. abortus* spread in elk and whether they can be targeted by any management actions; (2) estimate the risk of elk-cattle contact and *B. abortus* transmission, and the factors that can mitigate that risk and ideally eliminate transmission; and (3) refine and update models of disease dynamics to assimilate data for forecasting and informing alternative actions in active adaptive management.

Genetic and serological data from elk suggest that *B. abortus* has primarily spread in northwestern and northeastern directions from the Wyoming feedgrounds but with limited spread into southern Wyoming and Idaho. Further work is needed to predict the future rate and direction of *B. abortus* spread in elk, identify factors that may limit that progression, and subsequently determine possible management actions that can

Overall Findings, Conclusions, and Recommendations

target those factors. It will be important to design a study with an appropriate level of surveillance to further understand how brucellosis is self-sustaining in elk populations outside the feedgrounds. Collecting and establishing a repository of genetic isolates of *B. abortus* from elk and collecting samples of elk DNA would be useful.

Currently there are few predictors of where and when transmission from elk to cattle is likely to occur, and the effectiveness of local efforts to mitigate that risk is unknown. Measuring cattle risk at local and regional scales is critical to devising management actions that mitigate that risk. Case-control studies investigating why some ranching properties have had more elk to cattle transmission than others would help to elucidate whether there are local herd plans that are associated with lower risks despite similar broader scale transmission risks (e.g., elk density and seroprevalence). Further work on estimating the risk of elk-cattle contact and transmission and the factors that can mitigate that risk are critical to achieving the ideal of eliminating transmission into cattle.

6.2 Economic and Risk Analysis

Although there have been economic studies on the producer level, there has not been a bioeconomic analysis on comprehensive disease management strategies for the GYA as a system. Such an analysis would be critical in determining the costs and benefits of options as part of a decision-making framework. However, a number of knowledge gaps currently limit the ability to conduct a comprehensive analysis.

Recommendation 7B: To inform elk management decisions, high priority should be given to studies that would provide a better understanding of economic risks and benefits. It is critical to understand the following to conduct a comprehensive bioeconomic analysis:

- Information on values associated with GYA wildlife. This includes use values stemming from hunting, park visitation, wildlife viewing inside and outside Yellowstone and Grand Teton National Parks, and non-use values related to conservation of wildlife stocks. This would also include an evaluation of management actions perceived as undesirable, such as supplemental feeding, biobullets (which are no longer used), mass culls, and culls within YNP boundaries, including a temporal component of those actions (e.g., whether short-term culling for long-term goals might be acceptable).
- Information on social and private incentives for separating cattle from elk, both on private lands (hazing) and public lands (e.g., spatial-temporal grazing decisions).
- Information on incentives of other landowners to manage lands for elk habitat/refuge.
- Information about the costs and the effectiveness of the various actions (even as basic as vaccination) for reducing transmission and at various levels of effort.

6.3 Land Use

Land use changes have likely contributed to changes in elk numbers and distributions. As previously noted, land acquisitions by owners who discourage or prohibit access by hunters create elk refugia from hunting, which potentially contributes to larger elk populations and increased numbers of large elk aggregations. These population changes could enhance brucellosis transmission and reservoir maintenance independent of bison. Land use decisions by both livestock producers and natural resource agencies that control grazing allotments (such as the U.S. Forest Service and the DOI Bureau of Land Management) may impact the risk of transmission from wildlife to cattle and domestic bison. Similarly, the risk of transmission is impacted by the locations of elk feedgrounds relative to the spatial and temporal distributions of elk and cattle. However, there are limited data on the drivers of land use changes and how these changes contribute to the maintenance and spread of brucellosis in the GYA. A better understanding of these drivers and their impacts would be useful to inform land use policy as well as land owner and management agency actions to reduce risk of *B. abortus* transmission.

Revisiting Brucellosis in the Greater Yellowstone Area

Recommendation 7C: Studies and assessments should be conducted to better understand the drivers of land use change and their effects on *B. abortus* transmission risk. The studies should be designed to determine how changes in land use contribute to altered elk numbers and distributions; how land use changes affect the spread and maintenance of brucellosis in elk throughout the GYA; and how the spatial distributions of livestock producers, grazing allotments, and elk contribute to risks of elk to cattle transmission. Increased understanding of land use changes and their effects on elk distributions and interactions with livestock will facilitate the development of resource management approaches and policies that minimize *B. abortus* transmission risks.

6.4 Elk Diagnostics

Elk diagnostic testing will become increasingly important in the future as evidence suggests an expansion of *B. abortus*-infected elk ranges beyond current DSAs, transmission of *B. abortus* from elk to cattle, and maintenance in elk populations outside of the winter feedgrounds in Wyoming. While assays for testing of cattle for *Brucella* infection have a long history of success in effectively identifying *B. abortus* positive cattle, none of the current diagnostic assays have optimal characteristics for rapid, sensitive, and specific determination of disease status in elk. This is especially important due to the particular challenges in handling elk, obtaining specimens, and holding animals in pens until testing is completed.

Recommendation 7D: Priority should be given to developing assays for more accurate detection of *B. abortus*-infected elk, optimally in a format capable of being performed pen-side to provide reliable rapid results in the field.

6.5 *Brucella* Genetics

Although infection biology of *B. abortus* is better understood now than in 1998, there are still a number of major knowledge gaps in ruminants. Infection biology studies in elk, bison, and cattle have been largely neglected and have been greatly limited by onerous Select Agent requirements, the lack of large animal biocontainment facilities, and the substantial costs for large animal experiments.

It is important to note that scientific research in understanding brucellosis and progress in brucellosis diagnostics and vaccines has been hampered by the Select Agent Rule (implemented in 1997), which requires *B. abortus* to be handled, stored, transported, and distributed with significant restrictions. These restrictions have increased the cost of brucellosis research and have constrained brucellosis research in elk and bison to two U.S. laboratories. The higher cost of research and limited number of facilities capable of conducting brucellosis research also deters the next generation of scientists from pursuing research in brucellosis. Thus, the committee is supportive of current proposals and measures being taken to remove *B. abortus* from the Select Agent List.

Recommendation 7E: Research should be conducted to better understand the infection biology of *B. abortus*. To do so would require collecting *B. abortus* isolates from GYA elk, bison, and cattle and conducting comparative genomic analyses of those isolates to understand the underlying mechanisms for its adaptation in elk as a primary and likely self-sustaining host. It would also be useful to establish a biorepository of samples (e.g., serum, tissues, *B. abortus* isolates, DNA, RNA) with relevant metadata. Such a repository would have significant research value for future researchers to understand host and pathogen genetic characterization. A multiuser oversight group would be needed to manage the biorepository's acquisition, cataloging, and use of valuable samples for vaccine research and diagnostic test development.

Overall Findings, Conclusions, and Recommendations

6.6 Elk Immunology

Compared to bison and cattle, little is known about the elk protective immune response, and even less is known about genetic susceptibility to *B. abortus*. Unless more research is conducted on elk immunology and genetics, development of a safe and effective elk vaccine will remain a distant goal.

Recommendation 7F: To aid in the development of an efficacious vaccine for elk, studies should be conducted to understand elk functional genomics regulating immunity to *B. abortus*.

6.7 Vaccine and Vaccine Delivery System

The development of a more effective vaccine for each of the three ruminant species involved in maintenance and transmission of *B. abortus* in the GYA would significantly enhance progress in controlling brucellosis in the GYA. The development of an effective vaccine for elk, including an acceptable method of delivery, would be a major advance in expanding adaptive management options for eliminating brucellosis in domestic species. There are currently no effective brucellosis vaccines for elk, and current approved vaccines for bison and cattle have limited effectiveness against infection.

Recommendation 7G: The research community should (1) develop an improved brucellosis vaccine for cattle and bison to protect against infection as well as abortion, and (2) develop a vaccine and vaccine delivery system for elk. These new vaccines should consider mucosal vaccination approaches and possibly incorporate a microencapsulation approach to improve vaccine efficacy. In addition, any new vaccine should be compatible with parenteral or oral delivery and should allow differentiation of infected from vaccinated animals (DIVA compatible). An effective vaccine for elk is needed to control brucellosis in the GYA. However, delivery of vaccines to wide-ranging animals such as elk and bison over varied terrain would be logistically challenging. A vaccine delivery system that depends on baiting would be needed. Furthermore, assessments are needed to determine how effective vaccines and vaccine delivery systems would be implemented.

7. CONCLUDING REMARKS

Since 1998, significant changes have occurred in understanding and managing brucellosis in the GYA. Even over the course of the committee's review, there were rapid changes in management practices and new cases of brucellosis in cattle and domestic bison, which re-emphasizes the difficulty in handling this complex and expanding problem. Brucellosis was eliminated from cattle in the United States after nearly a century of dedicated funding and resources from USDA, states, and livestock producers. With increasing incidence of brucellosis in cattle and domestic bison herds in the GYA in the past few decades due to transmission from elk, significant resources are needed to address a problem that is expanding in scale and scope; without the changes and investments necessary to aggressively address this problem in a coordinated and cost-effective manner, brucellosis will likely spread beyond the GYA into other parts of the United States resulting in serious economic and potential public health consequences. Efforts to reduce brucellosis in the GYA will depend on significant cooperation among federal, state, and tribal entities and private stakeholders as they determine priorities and next steps in moving forward. The report's intent is to be useful for decision makers and stakeholders as they address the challenging matter of brucellosis in the GYA.

REFERENCES

Maichak, E.J., B.M. Scurlock, P.C. Cross, J.D. Rogerson, W.H. Edwards, B. Wise, S.G. Smith, and T.J. Kreeger. 2017. Assessment of a strain 19 brucellosis vaccination program in elk. *Wildlife Society Bulletin* 41:70-79.

Revisiting Brucellosis in the Greater Yellowstone Area

Peterson, M.N., A.G. Mertig, and J. Liu. 2006. Effects of Zoonotic Disease Attributes on Public Attitudes Towards Wildlife Management. *Journal of Wildlife Management* 70(6):1746-1753.

Appendix A

Biographical Sketches of Committee Members

Terry F. McElwain (NAM), *Chair*, is a Regents Professor Emeritus in the Paul G. Allen School for Global Animal Health in the College of Veterinary Medicine at Washington State University. He served for 22 years as the Executive Director of the Washington Animal Disease Diagnostic Laboratory, and was a co-founder of the School for Global Animal Health at Washington State University. Dr. McElwain is the Past President of the American Association of Veterinary Laboratory Diagnosticians, and he serves on the Board of Directors of the World Association of Veterinary Laboratory Diagnosticians. He was a key architect in the creation and development of the National Animal Health Laboratory Network. Dr. McElwain is an elected member of the National Academy of Medicine and a Fellow in the American Association for the Advancement of Science. He is member of the board of directors for the Foundation for Food and Agricultural Research, which was authorized by Congress as part of the 2014 Farm Bill. Dr. McElwain chaired the National Research Council's (NRC's) Committee on an Analysis of the Requirements and Alternatives for Foreign Animal and Zoonotic Disease Research and Diagnostic Laboratory Capabilities. He has also served on the NRC's Committee on Assessing the Nation's Framework for Addressing Animal Diseases and on the Institute of Medicine and the NRC's Committee for Achieving Sustainable Global Capacity for Surveillance and Response to Emerging Diseases of Zoonotic Origin. Dr. McElwain has a long and established research record in the field of veterinary infectious diseases, especially those of agricultural animals. He received his D.V.M. (1980) from the College of Veterinary Medicine at Kansas State University and his Ph.D. (1986) from Washington State University.

L. Garry Adams is a Senior Professor and the former Associate Dean of Research and a Professor of Veterinary Pathology at the College of Veterinary Medicine and Biomedical Sciences at Texas A&M University. Dr. Adams has performed research on brucellosis for almost four decades such that 90 of his 270 refereed publications are focused on brucellosis in livestock and wildlife. The spectrum of his brucellosis research experience extends from the basic molecular pathogenesis of the brucellosis to genetic disease resistance against brucellosis to developing applied diagnostic assays and preventive vaccines for domestic animals and wildlife, including elk and bison of the Greater Yellowstone Area of the United States. Research findings of the team led by Dr. Adams have been actively implemented to improve the scientific basis of the national and international animal health regulatory programs for brucellosis. Dr. Adams is a scientific reviewer or editor for 21 national and international research journals. Dr. Adams has served on the National Research Council's Committee on the Department of Defense's Programs to Counter Biological Threats and Committee on Biodefense at the U.S. Department of Defense. Dr. Adams received his D.V.M. from Texas A&M University's School of Veterinary Medicine, his Ph.D. in veterinary pathology from Texas A&M University, and his B.S. in animal science from Texas A&M University.

Cynthia L. Baldwin is a Professor in the Department of Veterinary and Animal Sciences at the University of Massachusetts Amherst and a member of the Cellular and Molecular Biology graduate program. Dr. Baldwin has been an investigator in the area of cellular immunology for more than 30 years. Her research has focused on cellular responses to bacterial and protozoan pathogens of humans and livestock, including *Brucella*, *Leptospira*, *Mycobacteria*, and *Theileria*. The lab also studied *Brucella abortus* to evaluate how some animals, but not others, successfully control infections by intracellular pathogens. Dr. Baldwin was

Revisiting Brucellosis in the Greater Yellowstone Area

named the 2013-2016 Distinguished Veterinary Immunologist by the International Union of Immunological Societies. She is a member of the American Association of Immunologists and has served as president of the American Association of Veterinary Immunologists and as chair of the international organization Brucellosis Research Workers. Currently she is on the veterinary immunology committee of the International Union of Immunological Societies, on the Technical Committee of AgResults' \$30 million prize to generate a new vaccine for brucellosis in small ruminants, a section editor of the *Journal of Immunology*, and on the editorial board of the journals *Veterinary Immunology and Immunopathology* and *Infection and Immunity*. She served as a Jefferson Science Fellow for the U.S. Department of State and works specifically within the U.S. Agency for International Development, traveling to Africa in conjunction with the Feed the Future program to increase world food security, which includes a research agenda for reducing infectious diseases in livestock. Dr. Baldwin received her Ph.D. (1983) in immunology from Cornell University.

Michael B. Coughenour is a Senior Research Scientist at the Natural Resource Ecology Laboratory and the UV-B (ultraviolet solar radiation) Monitoring and Research Program at Colorado State University. His primary research activities have focused on ecosystems dominated by large herbivores. He has developed three ecosystem models, including the SAVANNA landscape model. He carried out research on the Serengeti grazing ecosystem of Tanzania, using simulation modeling and experimental studies to determine how the ecosystem supports the world's largest ungulate herds. He was a joint principal investigator on the South Turkana Ecosystem Project, investigating a native pastoral ecosystem in northern Kenya. He has carried out several major modeling and field studies of grazing ecosystems and assessments of ungulate carrying capacities in Yellowstone and Rocky Mountain National Parks, the Pryor Mountain Wild Horse Range, and the Teton-Jackson elk range. He was principal investigator of a large project to use integrated assessments to assess wildlife-livestock interactions in East Africa. He has been involved in research on pastoral and grazing ecosystems in Tanzania, Kenya, South Africa, Australia, Inner Mongolia, Kazakhstan, Venezuela, Canada, and other locations around the world. Dr. Coughenour received his Ph.D. from Colorado State University specializing in systems ecology and biogeochemistry of grassland ecosystems.

Paul C. Cross is a research wildlife biologist with the U.S. Geological Survey. His research integrates field ecology, epidemiology, and statistics. He collaborates with a diverse team to also include genetics, microbiology, and remote sensing experts to address wildlife disease, conservation, and management issues. There are two central themes in his research: (1) the integration of empirical data and mathematical modeling, and (2) the effects of host behavior on disease dynamics. Currently, his research focuses on several wildlife disease issues around the Greater Yellowstone Ecosystem, including brucellosis, chronic wasting disease, canine distemper and sarcoptic mange. His expertise is in the areas of disease ecology, ungulates, epidemiological models, and statistical analyses of observational datasets. Dr. Cross received his Ph.D. (2005) in environmental science, policy, and management from the University of California, Berkeley, and his B.A. (1998) in environmental science from the University of Virginia, Charlottesville.

Richard D. Horan is a Professor in the Department of Agricultural, Food, and Resource Economics at Michigan State University (MSU) and a 2014 recipient of MSU's William J. Beal Outstanding Faculty Award. Dr. Horan teaches natural resource economics, and his research interests are in the areas of environmental and natural resource economics management and policy design. In particular, he concentrates on understanding feedbacks between economic and ecological systems and how these affect management opportunities. His interests are in the management of endangered and threatened species and ecosystems, the co-evolution of economic and ecological systems, prevention and control of invasive alien species, infectious disease in wildlife, and agricultural pollution and conservation. Dr. Horan has served as an editor of *Resource and Energy Economics* (2010-2014) and as an associate editor of the *American Journal of Agricultural Economics* (2008-2011) and *Natural Resource Modeling* (2007-2008). In 2015, he published "Managing Dynamic Epidemiological Risks Through Trade," "Managing the Endogenous Risk of Disease Outbreaks with Non-Constant Background Risk," and "Self-Protection, Strategic Interactions, and the Relative Endogeneity of Disease Risks." His 2014 publications include "Interspecies Management and

Appendix A

Land Use Strategies to Protect Endangered Species” and “Merging Economics and Epidemiology to Improve the Prediction and Management of Infectious Disease.” Dr. Horan received his Ph.D. and M.A. from The Pennsylvania State University and his B.S. from Appalachian State University.

David A. Jessup is an associate researcher and a wildlife veterinarian with the Wildlife Health Center at the University of California, Davis, School of Veterinary Medicine. He is also the Executive Manager of the Wildlife Disease Association. Dr. Jessup was the first veterinarian hired by the California Department of Fish and Game, for which he served as a clinical veterinarian, pathologist, researcher, field veterinarian, and supervisor for more than 33 years. During that time, he worked on a wide array of North American terrestrial and aquatic issues and conservation medicine issues and was also involved in projects in Mexico, Africa, and India. As an instructor with International Wildlife Veterinary Services, he taught wildlife capture and handling courses nationwide and in several other countries. Dr. Jessup is a Diplomate of the American College of Zoological Medicine and a Certified Wildlife Biologist with The Wildlife Society. Dr. Jessup has authored or co-authored more than 250 peer-reviewed and/or popular publications and book chapters. He has also served in numerous leadership roles, including president and vice president of the Wildlife Disease Association and twice president of the American Association of Wildlife Veterinarians. He also served on and chaired the American Veterinary Medical Association Committee on Environmental Issues. Dr. Jessup received his D.V.M. (1976) from Washington State University, Master of Preventive Veterinary Medicine degree (1984) from the University of California, Davis, and B.S. (1971) in zoology from the University of Washington.

Dustin P. Oedekoven is the State Veterinarian for South Dakota and the Executive Secretary for the South Dakota Animal Industry Board. He directs the board’s responsibilities in animal and public health and food safety. Dr. Oedekoven is a member of the U.S. Animal Health Association (USAHA) and currently serves as the chairman of the USAHA Bovine TB committee. He also serves on a number of review and advisory committees, including the U.S. Department of Agriculture National Advisory Committee on Meat and Poultry Inspection and the Agricultural Technical Advisory Committee for Trade in Animals and Animal Products. He previously worked in a private veterinary practice in Wyoming. He is a Diplomate of the American College of Veterinary Preventive Medicine. Dr. Oedekoven received his D.V.M. (2002) from Iowa State University and his B.S. in agricultural science from South Dakota State University.

David W. Pascual is a Professor of mucosal immunology at the University of Florida’s College of Veterinary Medicine. His laboratory is focused on understanding the basic tenets of mucosal immunology and their application to improve targeted mucosal vaccine delivery. Dr. Pascual and his colleagues are developing and testing brucellosis vaccine varieties in livestock with the hope that humans will ultimately benefit as well. He recently developed live vaccine prototypes for brucellosis that appear to confer high levels of protection in some animals against pulmonary *Brucella* infections. Dr. Pascual has served on more than 40 National Institutes of Health grant review panels with emphasis on mucosal immunology and infectious disease research. He previously served from 2002-2006 as a mucosal immunology section editor for *The Journal of Immunology*, and he currently serves as one of the editors for *Clinical and Vaccine Immunology*, a journal of the American Society for Microbiology. Dr. Pascual was previously at Montana State University’s Department of Immunology & Infectious Diseases. Dr. Pascual received his Ph.D. (1987) and M.S. (1985) from the University of Mississippi Medical Center.

Valerie E. Ragan is the Director of the Center for Public and Corporate Veterinary Medicine with the Virginia-Maryland College of Veterinary Medicine (VMCVM), which trains veterinary students for public practice careers. Dr. Ragan also continues to work around the world on the control and eradication of brucellosis and on projects related to veterinary capacity building. Prior to joining VMCVM, she was the president of an agriculture and veterinary consulting company in Washington, DC, where her activities included resolving animal health issues such as disease control, eradication, and surveillance, as well as

Revisiting Brucellosis in the Greater Yellowstone Area

international veterinary capacity building. Dr. Ragan previously served as the Assistant Deputy Administrator of the Veterinary Services program in the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (USDA-APHIS). In that role, she primarily served as the national animal health surveillance system coordinator for veterinary services, overseeing the development and implementation of a comprehensive, integrated national surveillance system and creating the National Surveillance Unit. During her tenure at USDA-APHIS, she also served as Senior Staff Veterinarian and National Brucellosis Epidemiologist at USDA-APHIS, with national responsibility related to brucellosis eradication in the United States. She has assisted with the development and evaluation of brucellosis eradication efforts internationally as well by providing training and consultation on-site. Dr. Ragan also serves on the Brucellosis Committee and the Brucellosis Scientific Advisory Subcommittee for the U.S. Animal Health Association. She also serves on the Consortium for the Advancement of Brucellosis Science in the United States. Dr. Ragan received her D.V.M. (1983) from the University of Georgia and has taken graduate-level courses on biostatistics and epidemiology at the University of Michigan School of Public Health.

Glynn T. Tonsor is a Professor of agricultural economics at Kansas State University. Dr. Tonsor's current efforts are primarily devoted to a range of integrated research and extension activities, with particular focus on the cattle/beef and swine/pork industries. His broader interests cover aspects throughout the meat supply chain, ranging from production-level supply issues to end-user consumer demand issues. Dr. Tonsor joined the K-State agricultural economics faculty as an assistant professor in March 2010 and was previously an Assistant Professor in the Department of Agricultural, Food, and Resource Economics at Michigan State University from 2006-2010. Dr. Tonsor received his Ph.D. (2006) in agricultural economics from Kansas State University and his B.S. (2001) in agriculture business-finance from Missouri State University.

Appendix B

Open Session Meeting Agendas

FIRST MEETING AGENDA

July 1-2, 2015
Montana State University
Strand Union Building
Ballroom A

WEDNESDAY, July 1

- | | |
|----------------|---|
| 1:00–1:15 p.m. | Welcome and Introductions
<i>Terry McElwain, Committee Chair</i> |
| 1:15–1:30 p.m. | National Academy of Sciences Study Process and Committee’s Statement of Task
<i>Peggy Yih, Study Director</i>
(15-minute presentation) |
| 1:30–2:15 p.m. | Charge to the Committee from the Sponsor; Regulatory Oversight of Brucellosis Under USDA Jurisdiction
<i>P. Ryan Clarke, U.S. Department of Agriculture’s Animal and Plant Health Inspection Service (USDA-APHIS)</i>
(10-minute to discuss Statement of Task + 5-min Q&A, 15-min presentation on USDA mandate + 15-min Q&A) |
| 2:15–3:15 p.m. | Overview of Previous Work Conducted by the National Park Service on Brucellosis in the Greater Yellowstone Area; Status of Ongoing and Future Activities
<i>Superintendent Dan Wenk and P.J. White, National Park Service</i>
(40-minute presentation, 20-min Q&A with committee) |
| 3:15–3:30 p.m. | Break |
| 3:30–5:00 p.m. | Montana’s State and Regional Efforts on Brucellosis in the Greater Yellowstone Area

<i>Perspective from the Department of Livestock</i>
<i>Christian MacKay and Eric Liska, Montana Department of Livestock</i>
(30-minute presentation, 15-min Q&A with committee) |

Revisiting Brucellosis in the Greater Yellowstone Area

Perspective from the Department of Fish, Wildlife & Parks
Quentin Kujala, Kelly Proffitt, and Jennifer Ramsey,
Montana Department of Fish, Wildlife & Parks
 (30-minute presentation, 15-min Q&A with committee)

5:00–5:25 p.m. **Public Comments**
 Please register ahead of time

5:25–5:30 p.m. **Chair’s Closing Remarks for Day 1**
Terry McElwain, Committee Chair

5:30 p.m. **Adjourn Meeting for Day 1**

THURSDAY, July 2

8:30–8:45 a.m. **Welcome and Introductions**

8:45–9:15 a.m. **A Genomic Assessment of Brucellosis Transmission Dynamics in the Greater Yellowstone Ecosystem**
Pauline Kamath, U.S. Geological Survey

9:15–9:45 a.m. **Environmental Persistence of *Brucella abortus* in the Greater Yellowstone Area, and Wildlife Management and Conservation Practices**
Keith Aune, Wildlife Conservation Society

9:45–10:15 a.m. **Elk Ecology and Elk-Wolf Dynamics in Northern Yellowstone**
Dan MacNulty, Utah State University

10:15–10:30 a.m. **Break**

10:30–11:00 a.m. **Native American Bison Management and Practices**
Jim Stone, Inter Tribal Buffalo Council

11:00–11:30 a.m. **Impact of Brucellosis on Montana Livestock Production**
Errol Rice, Montana Stockgrowers Association

11:30–11:55 a.m. **Public Comments**
 Please register ahead of time

11:55 a.m.–12:00 p.m. **Chair’s Closing Remarks**
Terry McElwain, Committee Chair

12:00 p.m. **Adjourn Open Session**

YELLOWSTONE NATIONAL PARK FIELD TRIP
September 14, 2015

8:30 a.m. **Meet at the Carbella Boat Launch**
 NAS staff to check photo IDs of confirmed participants

Appendix B

8:45 a.m.	Depart via bus
8:45–9:00 a.m.	Carbella Scale of management issue; Elk populations and migration patterns; Risk of elk comingling with livestock; Northern management area for bison
9:30–10:00 a.m.	Stephens Creek Bison migration to northern boundary; Culling, testing, and vaccination
10:30–10:45 a.m.	Mammoth Bathroom Break at Yellowstone Center for Resources
11:00–11:15 a.m.	Blacktail Deer Plateau Bison seasonal use patterns
12:00–1:15 p.m.	Buffalo Ranch Lunch/Bathroom History of bison management; Importance of Yellowstone bison; Importance of wildlife viewing and tourism to area
2:45–3:15 p.m.	Corwin Springs USDA-APHIS bison pens and fertility control study
3:30 p.m.	Return to Carbella Conclude tour

SECOND MEETING AGENDA

September 15-16, 2015

Jackson Lake Lodge

Moran, WY

Grizzly Room

TUESDAY, September 15

9:15–9:30 a.m.	Welcome and Introductions, Summary of Yellowstone Field Trip <i>Terry McElwain, Committee Chair</i>
9:30–9:45 a.m.	National Academy of Sciences Study Process and Committee's Statement of Task <i>Peggy Yih, Study Director</i>
9:45–10:15 a.m.	A Century of Supplemental Feeding on the National Elk Refuge, Implications for Brucellosis Management in Elk and Bison <i>Eric Cole, U.S. Fish & Wildlife Service</i> (20-min presentation, 10-min Q&A with committee)
10:15–10:45 a.m.	Resource Management and Brucellosis in Grand Teton National Park <i>Sue Consolo-Murphy, National Park Service</i> (20-min presentation, 10-min Q&A with committee)

Revisiting Brucellosis in the Greater Yellowstone Area

- 10:45–11:00 a.m. **Break**
- 11:00–11:30 a.m. **USDA-APHIS Brucellosis Research Efforts**
Jack Rhyan, USDA-APHIS
 (20-min presentation, 10-min Q&A with committee)
- 11:30 a.m.–12:00 p.m. ***B. abortus* Vaccination and Diagnostics in Cattle, Bison, and Elk**
Steven Olsen, USDA Agricultural Research Service
 (20-min presentation, 10-min Q&A with committee)
- 12:00–12:30 p.m. **Brucellosis Surveillance**
Don Herriott for Brian McCluskey, USDA-APHIS
 (20-min presentation, 10-min Q&A with committee)
- 12:30–1:45 p.m. **Lunch on your own**
(Committee working lunch in closed session)
 Doors will close at 12:45 p.m. for committee’s closed session.
 Doors will reopen at 1:30 p.m. for the public.
- 1:45–2:15 p.m. **Cattle Grazing Allotments and Potential Impact of Intervention Strategies in the Bridger-Teton National Forest**
Tricia O’Connor, U.S. Forest Service
 (20-min presentation, 10-min Q&A with committee)
- 2:15–3:45 p.m. **Wyoming’s State and Regional Efforts on Brucellosis in the Greater Yellowstone Area**

 Perspective from the Wyoming Livestock Board
Jim Logan, Wyoming Livestock Board
 (30-minute presentation, 15-min Q&A with committee)

 Perspective from the Wyoming Game & Fish Department
Hank Edwards and Brandon Scurlock, Wyoming Game & Fish Department
 (30-minute presentation, 15-min Q&A with committee)
- 3:45–4:00 p.m. **Break**
- 4:00–5:30 p.m. **Idaho’s State and Regional Efforts on Brucellosis in the Greater Yellowstone Area**

 Perspective from the Department of Agriculture
Debra Lawrence for Bill Barton, Idaho Department of Agriculture
 (30-minute presentation, 15-min Q&A with committee)

 Perspective from the Department of Fish and Game
Duston Cureton for Mark Drew, Idaho Department of Fish and Game
 (30-minute presentation, 15-min Q&A with committee)
- 5:30–5:55 p.m. **Public Comments**
 Please register ahead of time

Appendix B

5:55–6:00 p.m. **Chair’s Closing Remarks for Day 1**
Terry McElwain, Committee Chair

6:00 p.m. **Adjourn Meeting for Day 1**

WEDNESDAY, September 16

8:15–8:30 a.m. **Welcome and Introductions**
Terry McElwain, Committee Chair

8:30–9:00 a.m. **Efforts by the Wyoming Brucellosis Coordination Team and the Consortium for the Advancement of Brucellosis Science**
Frank Galey, University of Wyoming
 (20-min presentation, 10-min Q&A with committee)

9:00–9:30 a.m. **Brucellosis Diagnostics and Risk Assessment for Wildlife and Livestock**
Brant Schumaker, University of Wyoming
 (20-min presentation, 10-min Q&A with committee)

9:30–10:00 a.m. **Economic Costs of Brucellosis Prevention and Management in the Greater Yellowstone Area**
Dannele Peck, University of Wyoming
 (20-min presentation, 10-min Q&A with committee)

10:00–10:15 a.m. **Break**

10:15–10:45 a.m. **Applicability of the Wildlife Conservation Society’s AHEAD Program Approach for the Greater Yellowstone Area**
Mark Atkinson, Wildlife Conservation Society
 (20-min presentation, 10-min Q&A with committee)

10:45–11:15 a.m. **Challenges of Brucellosis Management for Wyoming Cattle Producers**
James Magagna, Wyoming Stock Growers Association
 (20-min presentation, 10-min Q&A with committee)

11:15–11:40 a.m. **Public Comments**
 Please register ahead of time

11:40–11:45 a.m. **Chair’s Closing Remarks**
Terry McElwain, Committee Chair

11:45 a.m. **Adjourn Open Session**

Revisiting Brucellosis in the Greater Yellowstone Area

THIRD MEETING AGENDA
November 10, 2015
National Academy of Sciences Building
2101 Constitution Avenue, NW, Washington, DC
Room 120

- 8:30–8:45 a.m. **Welcome, Introductions, and Goals for the Meeting**
Terry McElwain, Committee Chair
- 8:45–9:00 a.m. **National Academy of Sciences Study Process and Committee’s Statement of Task**
Peggy Yih, Study Director
- 9:00–10:00 a.m. **Brucellosis Disease Modeling for Management of Bison and Elk**
N. Thompson Hobbs, Colorado State University
(40-min presentation, 20-min Q&A with committee)
- 10:00–10:30 a.m. **Bison Conservation Genetics and Genomics**
James Derr, Texas A&M University
(20-min presentation, 10-min Q&A with committee)
- 10:30–10:45 a.m. **Break**
- 10:45–11:30 a.m. **Valuation of Elk Hunting and Viewing**
John Duffield, University of Montana
(30-min presentation, 15-min Q&A with committee)
- 11:30 a.m.–12:00 p.m. **History and Current Status of RB51**
Gerhardt Schurig, Virginia-Maryland College of Veterinary Medicine
(20-min presentation, 10-min Q&A with committee)
- 12:00–12:15 p.m. **Public Comments**
Please register ahead of time
- 12:15–12:30 p.m. **Chair’s Closing Remarks**
Terry McElwain, Committee Chair
- 12:30 p.m. **Adjourn Open Session**